On the epidemiology, biology and food-dependent reproduction of the feral pigeon (*Columba livia*)

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Summary

Millions of feral pigeons (*Columba livia*, Gmelin 1789) live in close association with the human population in our cities. They have managed to adapt extremely well to city life. The partial absence of an effective regulation by enemies and the rich food basis in urban habitats allows the development and maintenance of large feral pigeon populations. These, however, can cause various problems such as fouling with feces, and the transmission of pathogenic microorganisms and parasites to humans. While many wild-living species have a parasitic fauna comparable to that of feral pigeons, no other species lives as close to humans and offers that many possibilities of transmission. Feral pigeons breeding and roosting close to human lodgings thus pose a serious health risk, which is why many homeowners try to protect themselves by repelling the birds from their house facades, window ledges and balconies.

New pigeon proofing systems are regularly introduced onto the market, but scientific proof of efficacy and a statement regarding their use from the point of view of animal welfare is usually lacking. We therefore evaluated the effectiveness of two gel repellents on free ranging feral pigeons in an experimental pigeon loft. The gels used an alleged tactile or visual aversion of the birds, reinforced by additional sensory cues. This study concludes that both gels show a restricted, transient repellent effect, but fail to prove the claimed complete effectiveness. In addition, the adhesive effect of the gels conflicts with animal welfare concerns because gluing of plumage presents a serious risk to feral pigeons and also to other non-target birds. The repellent gels are therefore not suitable for feral pigeon management in urban areas.

Additionally, an overview of the most essential pigeon proofing systems is provided within the frame of this thesis. It discusses the advantages and disadvantages of the most widespread systems and further sets the focus on animal welfare issues. The overview points out that even initially harmless and animal friendly proofing systems might become dangerous to the birds over time if they are not regularly maintained. It further highlights how important it is to scientifically test each system before usage. Moreover, this outline supports the recommendation that each system should come with a proper installation and maintenance guide when it is introduced onto the market. If untested systems are being put to the test by unknowing end users, they might endanger the birds. Additionally, uninformed homeowners violate the animal protection law if a system harms an animal, even if this happens with no ill intent.

In a further study, we examined the effect of a sudden decrease in the natural food basis on the reproduction of a well-studied feral pigeon breeding colony. Despite the known fact that food shortage is a major source of reproductive failure in feral pigeons, it was still unclear at which phase of the reproductive cycle it reduces overall reproductive success. The findings of this study imply that the number of broods per pair decreased significantly under food reduction, while the hatching success remained more or less constant. However, a significantly greater number of nestlings died during the costly rearing phase. Results suggest that the high energy demand of the fast growing feral pigeon nestlings cannot be met under food scarcity. The decreased number of broods and the limited fledging success consequently reduce the total number of fledged young by more than half, which finally leads to a decrease in colony size.

Another negative side effect of large feral pigeon populations, maintained through the abundant anthropogenic nutritional basis in urban surroundings, is the overcrowding at breeding places. From an epidemiological point of view, these high population densities can increase the transmission of pathogenic microorganisms and parasites, such as the pigeon tick *Argas reflexus*. The medically and veterinary important *A. reflexus* usually feeds on pigeons, but if a natural host is not available, it also enters dwellings to bite humans who can respond with severe allergic reactions including anaphylactic shock. The pigeon tick is ecologically extremely successful due to certain outstanding morphological, physiological, and ethological features. Yet, until today, it was still unclear how it finds its hosts. In the main study, we tested different host stimuli, such as living nestlings as well as begging calls, body heat, smell, host breath and pigeon tick feces, under controlled laboratory conditions. Of all stimuli tested, only heat seemed to play a central role in host-finding. Subsequently, the crucial heat stimulus was tested under natural conditions within a pigeon loft. The results demonstrated that the host finding ability of *A. reflexus* is restricted to only a few centimeters. We concluded that this ectoparasite finds its host by random movements and recognizes it only shortly before direct contact is made. These findings are useful for the control of *A. reflexus* in infested apartments, both to diagnose an infestation and to perform successful monitoring after disinfestation.

The aim of this thesis was to provide important insights into the epidemiology, biology and food-dependent reproduction of the feral pigeon. With these findings we hope to contribute to the healthier coexistence of feral pigeons and humans in urban habitats.

Zusammenfassung

Millionen Strassentauben (*Columba livia*, Gmelin 1789) leben in unseren Städten und haben engen Kontakt zum Menschen. Sie haben sich extrem gut an das urbane Leben angepasst. Durch den teilweise fehlenden regulierenden Feinddruck, sowie durch die reichhaltige Nahrungsgrundlage im urbanen Habitat können sich grosse Strassentaubenpopulationen entwickeln und aufrechterhalten. Dies kann zu diversen Problemen, wie die Verschmutzung durch Kot und die Übertragung von pathogenen Mikroorganismen und Parasiten auf den Menschen führen. Viele wild lebende Tiere haben eine ähnliche Parasitenfauna wie die Strassentaube, jedoch lebt keine andere Art so nahe am Menschen und bietet derart viele Übertragungsmöglichkeiten. Strassentauben, die sich nahe am menschlichen Wohnbereich aufhalten, stellen eine ernstzunehmende Gesundheitsgefährdung des Menschen dar. Aus diesem Grund versuchen Hauseigentümer, sich selbst zu schützen, indem sie den Vögeln den Zugang zu ihren Häuserfassaden, Fenstersimsen und Balkonen verwehren.

Neue Taubenabwehrsysteme gelangen häufig auf den Markt ohne vorher auf ihre Wirksamkeit und ihre Verwendung unter dem Aspekt des Tierschutzes geprüft worden zu sein. Aus diesem Grund wurde die Wirkung von zwei Abwehrgelen in einem Versuchstaubenschlag untersucht. Der Abwehrmechanismus der Gele gegenüber Vögeln beruht auf vermeintlichen taktilen oder visuellen Aversionen, welche durch zusätzliche Sinneseindrücke verstärkt werden sollen. In dieser Studie konnte gezeigt werden, dass beide Gele die Tauben weder nachhaltig noch wirksam fernhielten. Da die untersuchten Abwehrmittel ausserdem das Gefieder von Vögeln verkleben können, verstossen sie gegen das Tierschutzgesetz und sind für die Anwendung gegen Strassentauben in urbanen Habitaten nicht geeignet.

Des Weiteren wurde im Rahmen dieser Arbeit ein Überblick der am häufigsten verwendeten Taubenabwehrsysteme erstellt. Die Vor- und Nachteile der wichtigsten Systeme wurden diskutiert. Darüber hinaus wurde jedes System bezüglich seiner Tierschutzgerechtigkeit bewertet. Dieser Überblick verdeutlicht, dass auch an sich harmlose und tierschutzkonforme Abwehrsysteme zu einer Gefahr für Tauben und andere Vögel werden können wenn sie falsch montiert oder nicht regelmässig gewartet werden. Zusätzlich ist zu empfehlen, Taubenabwehrsysteme einer wissenschaftlichen Prüfung zu unterziehen bevor sie in den Verkauf gelangen. Zudem sollte jedes System mit einer ordnungsgemässen Gebrauchs- und

Wartungsanweisung geliefert werden. Ungeprüfte Systeme, die von unwissenden Verbrauchern erst in der Praxis getestet werden, gefährden die Vögel unnötig. Des Weiteren wird darauf hingewiesen, dass uninformierte Käufer ihrerseits gegen das Tierschutzgesetz verstossen sobald ein Tier durch ein System Schaden nimmt, auch wenn dies ohne Vorsatz geschieht.

In einer weiteren Studie wurden die Folgen einer plötzlichen Nahrungsverknappung auf die Fortpflanzung einer Strassentaubenkolonie untersucht. Die Limitierung der Nahrungsmenge ist als einer der Hauptgründe für die Einschränkung der Reproduktion bei Strassentauben bekannt. Hingegen war immer noch unklar in welcher Phase des Reproduktionszyklus die Ernährungssituation auf den Fortpflanzungserfolg wirkt. Die Ergebnisse der Studie zeigen, dass die Anzahl der Gelege pro Brutpaar merklich abnimmt, während der Schlupferfolg auch unter einer Nahrungsverknappung weitgehend konstant bleibt. Zudem konnte nachgewiesen werden, dass mehr Nestlinge während der Aufzuchtphase sterben. Der hohe Energiebedarf der schnell wachsenden Strassentaubennestlinge kann unter Futterverknappung nicht mehr gedeckt werden. Die verringerte Anzahl der Gelege sowie die erhöhte Nestlingsmortalität führen dazu, dass die Anzahl flügger Jungtiere um mehr als die Hälfte abnimmt. Diese Regulationsmechanismen führen schlussendlich zu einem Populationsrückgang.

Ein weiterer negativer Nebeneffekt von grossen Strassentaubenpopulationen, die durch die reichhaltige anthropogene Nahrungsgrundlage im urbanen Lebensraum aufrechterhalten werden, ist die Überbelegung der Brutplätze. Aus epidemiologischer Sicht können diese hohen Populationsdichten die Übertragung von pathogenen Mikroorganismen und Parasiten, wie die Taubenzecke *Argas reflexus*, begünstigen. Die human- und veterinärmedizinisch bedeutsame Taubenzecke ernährt sich normalerweise von Taubenblut, kann aber auch den Menschen befallen, wenn ihr natürlicher Wirt fehlt. Menschen, die wiederholt von Taubenzecken gestochen werden, können gegebenenfalls schwere allergische Reaktionen aufweisen. *A. reflexus* ist aus ökologischer Sicht extrem erfolgreich, da sie über eine Reihe ausserordentlicher morphologischer, physiologischer und ethologischer Eigenschaften verfügt. Dennoch ist bis heute unklar wie Taubenzecken ihre Wirte finden. In der Hauptstudie wurde unter kontrollierten Laborbedingungen die Wirkung verschiedener Wirtsreize (lebende Nestlinge, Bettelrufe von Jungtieren, Körperwärme, Geruch, Atemluft des Wirtes und Kot von Taubenzecken) untersucht. Die Resultate zeigen, dass die Zecken vornehmlich auf Wärme reagieren. In weiteren Versuchen wurde der ausschlaggebende Wärmereiz unter natürlichen Bedingungen in einem Taubenschlag. Die Ergebnisse dieser Studie zeigen, dass

A. reflexus ihren Wirt nur über kurze Distanzen von wenigen Zentimetern orten kann. Taubenzecken dürften durch zufällige Bewegungen auf ihre Wirte treffen und erst in unmittelbarer Nähe auf Wärmereize reagieren. Die Resultate können auch praktisch umgesetzt werden, indem der im Rahmen dieser Arbeit entwickelte Wärmeapparat zum Nachweis von Taubenzecken, z.B. als Erfolgskontrolle nach einer Desinfestation, eingesetzt wird.

Ziel der vorliegenden Arbeit war es, verschiedene Aspekte des Taubenproblems von der Epidemiologie, über die Fortpflanzungsbiologie, bis hin zum Management der Strassentaube zu bearbeiten und praktische Lösungen zu entwickeln. Es ist sowohl im Interesse der Strassentaube, als auch des Menschen, einen optimalen Weg der Koexistenz zu finden. Ich hoffe, mit dieser Arbeit einen Beitrag dazu geleistet zu haben.

Chapter 1

General Introduction

1 General Introduction

Feral pigeons are descendants of the domesticated form of the wild living rock dove (*Columba livia*, Gmelin 1789). In its natural habitat, the wild living rock dove breeds in crevices and caves on rocky cliffs (Haag-Wackernagel, 1998), but the descendant feral pigeons managed to adapt extremely well to urban life in our cities. They are able to breed and roost on numerous structures such as house facades, balconies, window ledges and monuments, analogue to the natural cliff habitat of the rock dove (Haag-Wackernagel, 1998). In addition, the originally granivorous birds adjusted to an omnivorous diet and digest basically every food they can find (Haag, 1984). The birds are also able to quickly react to environmental changes due to some extraordinary physiological features regarding their reproduction. Several evolutionary strategies promote high reproduction rates in pigeons. These include two egg clutches, small eggs (Robertson, 1988), quick replacement of lost clutches (Johnston and Janiga, 1995), feeding the nestlings with the highly nutritious crop milk (Gillespie *et al.*, 2012), overlapping clutches (Burley, 1980; Hetmański and Wołk 2005), biparental care of the brood and all-season breeding under optimal feeding conditions (Häkkinen *et al.*, 1973; Johnston and Janiga, 1995). If conditions are ideal, all of these features allow a breeding pair to produce up to 12 young per year (Haag, 1987). The partial absence of an effective regulation by enemies and the rich urban food basis allows the development and maintenance of large populations. The feral pigeon world population is estimated to be 10–20 birds per city resident (Johnston and Janiga, 1995; Vater, 1998), which leads to a current valuation of 170–340 million individuals in the cities around the world (Haag-Wackernagel, 2010a). Since suitable nesting sites are rare in most cities, intense competition, overcrowding and intraspecific stress at breeding sites frequently arise when pigeon numbers are high. As with any pest species that occurs in large numbers, large feral pigeon populations can cause various problems as e.g. fouling with feces, material pests emigrating out of nests, as well as the transmission of pathogenic microorganisms and parasites to humans.

Figure 1: Feeding of feral pigeons in an urban habitat.
Feral pigeons strongly depend on intentional feeding by humans and their food waste. The abundant anthropogenic nutritional basis in cities and urban surroundings allows the maintenance of large populations.

Every pigeon produces 4–11 kg feces yearly (Vogel, 1997) soiling breeding areas, house facades, monuments, streets and other city sites. The overall damage per feral pigeon and year is estimated to be EUR 23.7–33.5, which equals approximately $US 27–38 (Zucconi *et al.*, 2003). In addition to the cost factor, feral pigeons are able to transmit diseases and parasites. So far 111 pathogenic agents and a total of 20 harmful arthropod species that can infest humans have been found in feral pigeon populations (updated according to Haag-Wackernagel and Moch, 2004; updated according to Haag-Wackernagel and Bircher, 2010). While many wild-living species have a parasitic fauna comparable to that of feral pigeons, no other species lives as close to humans and offers that many possibilities of transmission.

The most important ectoparasite that can be transmitted from feral pigeons to humans is the pigeon tick *Argas reflexus* (Haag-Wackernagel, 2008). The hematophagous ectoparasite inhabits the nesting and roosting sites of rock pigeons and feral pigeons. It naturally feeds on pigeons, but uses less preferred substitute hosts when pigeon density is low or when pigeons are completely absent. Due to the specific synanthropic environment of urban areas, wandering ticks penetrate into human lodgings and make humans their most common substitute hosts (Karbowiak and Supergan, 2007). While the infested birds mainly suffer from blood loss and irritation, bites in humans can have serious consequences. They not only cause local reactions, but in predisposed humans severe allergies and even anaphylactic shock with fatal outcome may occur (Buczek and Solarz, 1993). As an inhabitant of human buildings in central Europe, *A. reflexus* is predominantly an urban pest (Dautel *et al.*, 1999) that spends most of its life off-host, hidden in cracks and crevices. The ecological success of the pigeon tick is due to its extraordinary physiological features, as e.g. long life expectancy (Dautel and Knülle, 1997a), long-term starvation capability (Dautel *et al.*, 1999), high tolerance to temperature extremes (Dautel and Knülle, 1996; Dautel and Knülle, 1997b) and the capability of replenishing net water losses through absorption of water vapour from the atmosphere at relative humidities ≥ 75 % (Kahl, 1989; Dautel, 2001). In spite of the medical and veterinary importance of the pigeon tick, it is still unclear how *A. reflexus* actually finds its hosts.

In order to solve the feral pigeon problem, there are two principal options: citywide solutions aiming at the reduction of the pigeon population, or the protection of a certain building.

As for option one, a population reduction can either be achieved by simply increasing the mortality, decreasing the reproductive success or by reducing the ecological conditions responsible for the large populations. However, in the examples where killing alone, by whatever means, has been used, a permanent reduction in pigeon numbers has not been achieved (Feare, 2004). Limiting the reproductive success includes exchange of eggs with dummies, egg removal, collection of nestlings, use of chemosterilants and surgical sterilisation. However, the limitation of reproductive success is basically unenforceable in urban breeding colonies, because they are mostly hidden and difficult to reach, which makes it impossible to treat all of the birds of one city. All these methods seem, therefore, to be ineffective due to compensation by extremely high natality and immigration (Haag-Wackernagel, 2002). Instead, feral pigeon populations strongly depend on food abundance for maintenance and growth (Haag, 1984). A reduction in food supply thus leads to increased temporal and energetic investments in foraging, which in turn reduces reproductive effort and consequently decreases the number of individuals if immigration is unable to compensate. In our cities, the available food basis is intentionally supplied by pigeon feeders or as food waste, but feeding restrictions are difficult to establish. Only educating the public that intentional pigeon feeding ultimately harms the animals and is destructive regarding animal welfare has been shown to be effective (Haag-Wackernagel, 1993). Small and healthy feral pigeon stocks are achieved by reducing the anthropogenic food base in the urban ecosystem. Despite the fact that food shortage is a major source of reproductive decline in feral pigeons, it is still unclear at which phase of the breeding cycle it reduces overall reproductive success.

Regarding option two, many people try on their own to solve the feral pigeon problem by excluding the birds from their buildings, e.g. with the help of pigeon proofing systems. Protection of buildings in residential areas and city centers includes a large number of nonlethal systems that are supposed to repel, deter and exclude the birds. However, most of these systems either lack scientific proof of efficacy or fail to prove their alleged effectiveness if put to test (Stock and Haag-Wackernagel, 2014). Furthermore, these systems have rarely been assessed from the point of view of animal protection. Given the fact that highly motivated pigeons are able to overcome almost every system (Haag-Wackernagel, 2000), the effectiveness of new bird proofing products should be investigated critically. Also, one should keep in mind that these systems do not solve the pigeon problem but simply shift it from one house to another (Haag-Wackernagel and Stock, 2015).

In summary, feral pigeons represent interesting research objects. They populate every larger city worldwide and live in close association to humans. As a part of our everyday life, they offer important insights into epidemiological, biological and physiological questions of urban ecology.

1.1 Aims of this Thesis

The aim of this thesis is to contribute to a better understanding of the biology of feral pigeons. It focuses on different questions concerning the epidemiology, biology and food-dependent reproduction of the birds. The following central issues are covered within the framework of this thesis:

- Investigation of the deterring effect of gel repellents on feral pigeons
- Review of the most important pigeon proofing systems under the aspect of animal welfare
- Effect of food shortage on the reproduction of feral pigeons
- Host finding in the pigeon tick *A. reflexus*

To process these matters, they were separately investigated in one out of four manuscripts published independently of each other. These manuscripts are displayed in the following chapters.

Chapter 2 provides results of a study conducted in the experimental loft to evaluate the effectiveness of gel repellents on feral pigeons. The focus of this study was not only set on efficacy, but also included animal welfare concerns.

Chapter 3 offers an overview about the most essential pigeon proofing systems. It discusses the advantages and disadvantages of the most widespread systems.

Chapter 4 deals with the effect of a breakdown in the natural food basis on the reproduction of a well-studied feral pigeon breeding colony. It points out at which phase of the breeding cycle a food shortage reduces overall reproductive success.

Chapter 5 gives insight into the host finding of the pigeon tick *A. reflexus*. It describes the testing of different host related stimuli and how the pigeon tick reacted towards them. Furthermore, this chapter describes how *A. reflexus* reacts to relevant host stimuli when exposed to them in its natural habitat. At the end of this chapter, the results are linked to practical use in detection and prevention of human infestations.

The summarized main findings and the general conclusions are discussed in chapter 6.

The main focus of this work was originally set on the pigeon tick *A. reflexus*. As this ectoparasite is ecologically extremely successful and resistant to numerous unfavorable living conditions, it was difficult to examine it in experiments under laboratory conditions. It took some time to determine the final experimental setup and collect enough specimens for the trials. Due to this long, unexpected preliminary work, this thesis was extended to other topics including the testing and review of pigeon proofing systems and the reproduction of feral pigeons under food shortage as displayed in chapter 2–4.

All in all, a number of unsatisfying pretrials were performed before it was finally possible to answer the questions of the host finding behavior of *A. reflexus* described in chapter 5. As this preliminary work was crucial to the ultimate version of the experimental setup, but is not included in the officially published manuscript, a brief summary of those pretrials is listed in chapter 8.

1.2 Materials and Methods

All materials and methods used for the studies of this thesis are accurately described in the respective chapters. Here I introduce a description of the experimental pigeon loft and present the pigeon tick *A. reflexus*.

1.2.1 The Experimental Pigeon Loft

The city of Basel coordinates nine pigeon lofts within the “Pigeon Action of Basel” (“Basler Taubenaktion”). The program exists since 1988 and was implemented by the University of Basel, the city government and the Society for the Protection of Animals of Basel. The purpose of the pigeon lofts of Basel is not to regulate the city’s feral pigeon population. Instead, they have more of an educational purpose within the scope of the “Pigeon Action of Basel”. The interdisciplinary project focuses on educating the public that intentional pigeon feeding ultimately harms the animals and is destructive regarding animal welfare. The complicated ecological relationship between a purposely provided, large, anthropogenic food base and overcrowding in breeding colonies is explained through pamphlets, posters, news articles, as well as radio and television interviews. Furthermore, groups of school classes and conference participants are regularly guided through the experimental loft to offer a direct insight into the habitat of the birds. Moreover, the lofts are regularly cleaned of droppings, nesting material and carcasses, which would otherwise accumulate in the city. They thus cover an additional hygienic aspect. Altogether, the “Pigeon Action of Basel” and its lofts aim at a small and healthy feral pigeon stock. One of the nine pigeon lofts regularly serves as an experimental loft. It has been used for years to study and observe feral pigeons within their natural habitat. The experimental loft is situated in the St. Matthew Church, which is located in a residential district of Basel, Switzerland (47° 34' 2.1144" N, 7° 35' 34.8540" E). It has a build in perspex disc that separates the feral pigeons from a small anteroom.

Figure 2: St. Matthew Church and its experimental feral pigeon loft in Basel, Switzerland.
The experimental pigeon loft is situated in the St. Matthew Church, which is located in a residential district of Basel, Switzerland.

The separated anteroom offers the unique possibility of observing the birds in person or even monitoring them with the help of an installed video camera. The possibility of videotaping the birds without disturbing them by entering the loft allows fascinating insights into their behavior. The pigeons are free to enter and leave the loft at will. All pigeons using the lofts of the "Pigeon Action of Basel" live under natural conditions and are not offered any food or water. The pigeons inhabiting the experimental loft generally forage in the city and the surrounding area (Rose *et al.*, 2006). The direct access to free ranging feral pigeons enabled the performance of epidemiological, biological and food-dependent reproduction studies on an uninfluenced feral pigeon population in the middle of Basel.

1.2.2 Feral Pigeons Studied for this Thesis

About 75–100 feral pigeons permanently inhabit the experimental pigeon loft. As no population control (e.g. egg removal, euthanizing of pigeons) is undertaken in the experimental loft, the birds are free to breed and raise their young.

Figure 3: One-day-old feral pigeon nestlings.
Two newly hatched feral pigeons in the experimental loft of the St. Matthew Church in Basel, Switzerland.

Every six months, the resident pigeons are caught overnight, ringed and weighed. These nighttime controls offer an exceptional, constant overview of the population dynamics of the birds inhabiting the loft. All pigeons are ringed, either directly as nestlings or as immigrated adults, and registered in a database. Due to the regularly performed flock controls, the life history of every single bird living in the experimental loft is electronically covered. Fledglings and adults are free to stay in their home colony, or to leave the loft to join other breeding flocks. Furthermore, immigrated adults regularly establish themselves in the breeding colony of the experimental loft. This interface offers numerous opportunities for disease and parasite transmission with all other feral pigeon colonies of Basel.

All studies that were performed within the framework of this thesis were carried out on the feral pigeons and their ectoparasites in the here-described experimental loft. Furthermore, all experiments conducted for this thesis obtained animal experimental permission from the Cantonal Veterinary Office of Basel-Town, Switzerland. They conformed to Swiss law on animal welfare and caused only minor, if any, stress to the birds.

1.2.3 Pigeon Ticks Studied for this Thesis

The pigeon tick *A. reflexus* usually feeds on pigeons, but also enters human dwellings and bites humans if its natural host is not available. It is the most important ectoparasite, even the most significant health hazard posed by feral pigeons (Haag-Wackernagel and Bircher, 2010). This widespread ectoparasite is found in most feral pigeon populations. It is mainly active during the night and has four developmental stages: egg, larva, 2–4 nymphal phases and adult. From an epidemiological point of view, *A. reflexus* living in urban areas is dependent on feral pigeons. As the host-specific ectoparasite is not able to establish a population solely on human blood (Kemper and Reichmuth, 1941), an infestation can always be traced back to an animal host, in the urban environment almost exclusively feral pigeons. The infested birds suffer mainly from blood loss and irritation. In humans, bites of the pigeon tick may cause reactions ranging from local inflammations to severe allergies and even anaphylactic shock with fatal outcome in predisposed patients.

Figure 4: The pigeon tick *Argas reflexus* on its natural host.
A pigeon tick sucking blood on the breast of a young feral pigeon (left side). After the blood meal, the tick left a bleeding wound and a hematoma that could be seen for several days (right side).

In spite of the public health risk originating from the pigeon tick, it is still unclear how it finds its hosts. Due to the lack of knowledge, the tick's host finding abilities were tested under constant laboratory conditions. Subsequently, one of the tested stimuli turned out to be crucial and was hence confirmed to be relevant in host finding under natural conditions in the experimental pigeon loft.

All pigeon ticks that were used for this thesis hatched under experimental conditions from eggs laid by adults collected out of the experimental loft. The nocturnal pigeon ticks were collected out of cracks and crevices in the experimental pigeon loft. They were then individually stored in test tubes sealed with a fine net and kept under constant laboratory conditions. These ideal living conditions allowed the females in the test tubes to lay eggs out of which hundreds of larvae hatched. Each larval pigeon tick used for this thesis had thus identical living conditions before it was used in the host-finding experiments of chapter 5.

Chapter 2

Effectiveness of Gel Repellents on Feral Pigeons

Birte Stock & Daniel Haag-Wackernagel

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Article

Effectiveness of Gel Repellents on Feral Pigeons

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Simple Summary: Feral pigeons live in close association in urban areas. They constitute serious health risks to humans and also lead to high economic loss due to costly damage to buildings, historic monuments, statues and even vegetation. While numerous avian repellent systems are regularly introduced onto the market, scientific proof of efficacy and their use from the point of view of animal welfare is lacking. Therefore, two avian gel repellents were studied on free-living feral pigeons in this study. The focus was set on repellent efficacy and animal welfare concerns. This study's aim is to contribute to a better understanding of feral pigeon management in our cities.

Abstract: Millions of feral pigeons (*Columba livia*) live in close association with the human population in our cities. They pose serious health risks to humans and lead to high economic loss due to damage caused to buildings. Consequently, house owners and city authorities are not willing to allow pigeons on their buildings. While various avian repellents are regularly introduced onto the market, scientific proof of efficacy is lacking. This study aimed at testing the effectiveness of two avian gel repellents and additionally examined their application from animal welfare standpoint. The gels used an alleged tactile or visual aversion of the birds, reinforced by additional sensory cues. We mounted experimental shelves with the installed repellents in a pigeon loft and observed the behavior of free-living feral pigeons towards the systems. Both gels showed a restricted, transient repellent effect, but failed to prove the claimed complete effectiveness. Additionally, the gels' adhesive effect remains doubtful in view of animal welfare because gluing of plumage presents a risk to feral pigeons and also to other non-target birds. This study infers that both gels lack the promised complete efficacy, conflict with animal welfare concerns and are therefore not suitable for feral pigeon management in urban areas.

Keywords: capsaicin; *Columba livia*; contact gel; feral pigeon; optical gel; repellent gel

1. Introduction

The feral pigeon, the descendant of the domesticated form of the wild living Rock Dove (*Columba livia*), is a highly successful urbanophilic species, which occurs worldwide. With a domestication history of several thousand years [1], feral pigeons are well adapted to human environments. Due to the abundant feeding options in our cities, feral pigeons have expanded their originally granivorous diet to an omnivorous one [2]. In addition to the positive nutritional effects, cities with house facades, churches and statues offer an ideal environment for the birds. Pigeons that originally lived along coasts with cliffs now use numerous structures associated with urban buildings as roosting, resting, nesting and outlook spots. The close association of large feral pigeon populations and humans creates a human-wildlife conflict with serious health risks. With more than 100 human pathogenic microorganisms and 18 ectoparasites associated with feral pigeons [3,4], the epidemiological significance of these birds to humans is evident. Although the risk of zoonotic diseases caused by feral pigeons is rare, fatal cases have been reported [5]. Besides the medical risk, feral pigeons living in urban habitats also lead to high economic loss due to significant damage to buildings, historic monuments, statues and even vegetation [2]. The removal of pigeon droppings from buildings causes high costs [6]. With an individual pigeon producing around 4–11 kg of excrement each year [7], enormous quantities of pigeon droppings end up in every larger city of the world. This excrement offers a substrate for the growth of microorganisms that are able to destroy building materials [8].

In addition to these negative esthetic and hygienic aspects, the costs of feral pigeons living in urban environments are high. The estimated damages per feral pigeon per year including pollution of buildings, streets and places, as well as hygienic costs, agricultural costs and bird strikes range from 23.7€ to 33.5€ [9], which equals approximately $US 31 to 44. In the USA, the damage caused by feral pigeons has been estimated to $US 1.1 billion per year, not including environmental damage associated with the pigeons serving as reservoirs and vectors for diseases [10]. The relevance of pigeons is further pointed out by the number of about 22’500’000 hits when entering the words “pigeon problems” into the internet search engine Google (accessed 28 October 2013).

Frequently recommended solutions to solve the pigeon problems in residential areas and city centers include a large number of nonlethal systems that repel and exclude the birds from buildings and monuments. Repellents can be used to manipulate animal behavior in a way that an animal is motivated to avoid the consequences of the aversive signal [11]. In general, animal repellent systems can be of visual, acoustic, tactile, olfactory, or gustatory nature, or even combine several of these characteristics [11–17]. The business of production and installation of avian repellent systems involves the sales of millions of dollars worth of products in Europe and the USA [9,18,19]. While netting and other exclusion systems are successfully used against pigeons, these methods do not always seem to be an economic or practical option [20], and such eye-catching systems often distract from the architectural impression [21]. In particular, historic buildings are sensitive to pigeon droppings and difficult to protect from these birds. With the sheltered niches, crevices and ledges common to ornamental facades, such buildings offer ideal nesting and roosting habitats [22]. Several other proofing products promise an optimal integration in the esthetic impression of building facades since they are inconspicuously and discretely mounted onto the affected structure or area. Whereas for example netting and spikes repel the pigeons on the basis of exclusion via mechanical barriers, other innovative systems are often supposed to work with aversive cues that motivate the bird to avoid the treated spaces. These new systems, which are regularly introduced onto the market, promise to be the ideal solution to the problems caused by pigeons on buildings. They are supposed to be not only effective, but also inconspicuous, easy to mount and available at a competitive price. However, data to support the expected results of these new, inventive and allegedly persistently effective bird repellents is rare or inexistent. Furthermore, these new products have rarely been put to test under the point of view of animal welfare. Given the fact that highly motivated pigeons are able to overcome almost every system [19], the effectiveness of new bird repellent products should be investigated critically.

A reasonable feral pigeon management in urban areas requires very good knowledge of proofing and scaring systems and the reactions of the birds towards them. We therefore tested two nonlethal, food-grade, avian repellent gels that are supposed to combine an easy and discrete installation with 100% success in removing the birds from treated areas within less than a week. While one gel is based on the alleged tactile aversion of the birds to capsaicin, the other claims to function through a visual repellent effect that is reinforced by ingredients that are repulsive to the olfactory, gustatory and tactile senses of the birds.

The objective of our study was to assess the effectiveness of these two avian gel repellents by analyzing the behavior of feral pigeons when confronted with them. In addition to the efficacy of the products, we also focused on the gels from the point of view of animal welfare.

2. Materials and Methods

2.1. Study Area

We conducted our study in the pigeon loft of the St. Matthew Church, which is situated in a residential district of Basel, Switzerland (47.5671°N, 7.5930°E). The city of Basel is located in northwestern Switzerland, at the intersection of Switzerland, Germany and France. In August 2012 it counted around 170’000 inhabitants. The climate is continental and during the study period, average temperatures ranged from 20.7 °C in August to 10.7 °C in October.

The pigeon loft was situated above the nave of the church at a height of about 18 m above ground. Besides a floor space of 28 m^2, the loft had 39 nesting boxes and several roosting bars. We set a timer for constant diurnal rhythm of 9 hours and 30 minutes of light and 14 hours and 30 minutes of dark in the loft. The experiments were performed under natural conditions without offering any food or water. The pigeons used the loft exclusively for roosting and breeding. Their food was generally foraged in the surrounding area and the city [23].

2.2. Tested Bird Repellent Gels

Two avian repellent gels were tested on free-ranging feral pigeons: a contact gel and an optical gel. Both products are used in pest bird management programs to protect structures from birds. Since repellent products are continuously changing their names or reentering the market only slightly modified, we refrain from providing the names of the products and the manufacturers. Instead, the tested products stand for a specific but conventionally used kind of repellent system.

2.2.1. Contact Gel

As specified by the manufacturer, the contact gel included non-toxic, 100% natural ingredients and can be used to protect all kinds of indoor and outdoor surfaces of buildings, monuments and also statues against nuisance birds, especially pigeons. The gel contained 0.0357% capsaicin, which is the pungent element of red pepper [24]. According to the distributor, capsaicin causes a mild harmless irritation when being transferred onto the feet of the birds by landing on the treated areas. This sensory reaction to the gel is supposed to condition the pigeons to avoid the location. The clear, odorless and semi-solid gel was supplied in 300 mL cartridges and applied on the experimental shelves in a wave pattern at a stretch according to the application instructions. The distributor claimed that 100% of the bird population would be successfully removed within seven days of gel application, which was allegedly proven during rigorous testing carried out by the developers.

2.2.2. Optical Gel

The second bird repellent, which was examined, was an optical gel, sold by another distributor. According to the general product information, the gel is patented and contains food-grade natural oils. It is supposed to repel all birds from all indoor and outdoor structures without causing any harm to target animals. Ingredients in the product include polyisobutylene, grease lubrication, peppermint oil and cinnamon oil. According to the distributor, the gel is able to repel the pigeons visually because it is perceived as fire within the ultraviolet visual range of the birds. Furthermore, the distributor claimed that natural oils, which should be abhorrent to a bird’s senses of smell, taste and touch, reinforce the visual repellent effect. The gel was delivered in 250 mL cartridges with supplementary application dishes of 7 cm in diameter. We applied 15 g of the repellent gel in each dish as recommended in the manufacturer’s guidelines.

After consultation with the distributor who determined the number and location of dishes on the experimental shelves, we arranged eight dishes per shelf in two parallel rows of four dishes. The dishes covered a total of 17% of the shelves. The greatest distance between two dishes was 13 cm. According to the application guide, this distance referred to an area with high bird density. The manufacturer claimed that after two or three days even the most dominant birds would avoid the treated areas.

2.3. Study Animals

The feral pigeon colony used for this study contained about 85 birds with an average body weight of 322 g. Due to the fact that the pigeon loft was freely accessible to every feral pigeon in the surrounding area and the birds of our study were able to enter and leave the loft at will, fluctuation of the population was possible. We routinely caught, ringed and weighed the resident pigeons every six months. During the study period, one pigeon that hatched in the loft became integrated into the population, another adult pigeon immigrated and six pigeons, both adults and young, left the population. Due to the periodical flock controls and the cleaning of the pigeon loft twice a month, the pigeons were habituated to human presence. Even though all pigeons of the loft were ringed, either directly as nestlings or as immigrated adults, the small ring numbers were not recognizable on the video material. An unambiguous assignment of the observed reactions of the pigeons to a particular bird was thus not performed.

2.4. Experimental Design and Data Collection

We installed four experimental shelves of 0.6 m length and 0.3 m width as resting, roosting and outlook spots for the pigeons in the loft. Each shelf was attached onto the wall at right angles, offering the birds a convenient area to perch. The shelves were placed in a zigzag pattern at heights of 0.8 m to 1.6 m, about 1.3 m away from the nesting boxes on the adjacent wall. After the installation, the pigeons were given ten days to get used to the new structures in the loft. We performed our experiment in August–October 2012. It consisted of two main phases: a pretrial of 16 days and a trial phase of 26 days. We monitored the experiment with a video camera (JVC model GY-HM150E, Yokohama, Japan) at random dates each for 24 hours. On 27 August 2012, we started the pretrial phase during which we video recorded three out of 16 days in a weekly rhythm to get a base value for the daily use of the shelves without the installed repellents. The dishes in which the optical gel was applied were not mounted during the pretrial phase. The idea was to first create a natural scene with an ordinary structure frequently used by pigeons and not treated with any kind of repellent or uncommon system. Each of the gels was applied on two of the experimental surfaces, according to the distributor's guidelines, on 12 September 2012. However, the shelves and the wall on to which they were installed were thoroughly cleaned before application, as the products are said to only have full effectiveness when used on unsoiled structures, free from any bird excreta. We recorded 16 days of our 26 days trial phase, with the last recorded day being trial day 26. Due to methodological considerations, we eliminated the first trial day of the visual gel testing and restarted the experiment on the second day of recording. As a result, we excluded the first trial day from statistical analyses and assigned the actual second trial day as the first. Thus, the last recorded day of the visual gel testing was trial day 25.

In addition, the emissions and the lifetime of the excited states of the optical gel was measured as it is supposed to be perceived as fire within the ultraviolet visual range of the feral pigeons. The measurements were taken with the compact fluorescence lifetime spectrometer Quantaurus-Tau C11367-11 by Hamamatsu excited at a wavelength of 280 nm.

2.5. Animal Welfare Point of View

We conducted the experiments with the animal experimental permission of the Cantonal Veterinary Office of Basel-Town, Switzerland (authorization No. 2296). The study conformed to Swiss law on animal welfare. The permission allows experiments on animals causing mild stress, which corresponds to the severity Grade 1. According to Swiss animal welfare, severity Grade 1 studies include interventions and manipulations on animals for experimental purposes, which subject the animals to a brief episode of mild stress (pain or injury). Furthermore, it is claimed in Article 4(2) of the Swiss Animal Welfare Act that no person may, without justification, inflict pain, suffering, or injury upon an animal or cause it fear, or disregard the dignity of the animal in any other way. With this in mind, we first tested the pigeons' behavior towards the gels applied in nesting boxes during a test run. During this test run, the pigeons entered their nesting boxes in all cases. Apparently, the birds were not repelled by the gels due to their high motivation to repossess their breeding places. Furthermore, because the chances of nestlings and inexperienced juvenile birds getting into contact with the sticky gels were too high, the nesting boxes test run was canceled prematurely. For that reason we chose to test the repellent gels on new, rather unpopular, experimental shelves in heights starting at 0.8 m so that nestlings and badly flying juveniles were not able to smear the sticky products into their not yet fully grown plumage. With these low motivation structures, not being as fiercely contested as other areas in the loft, the risk of gluing of plumage of adult pigeons was further minimized.

2.6. Data Analysis

We evaluated the recorded behavior and analyzed the number of approaches and landings, as well as the time spent on the experimental shelves prepared with the two repellents for each recorded day. A successful repellent system reduces the number of birds using the protected structure by 100%. Although a general reduction might seem effective to non-experts, only a complete protection marks a successful repellent system. Even low numbers of pigeons still using and soiling the treated areas point out the failure of the repellent system. For the simple reason that even a single pigeon is able to transmit human pathogenic diseases, a repellent system should not only reduce the number of pigeons using a treated structure, but completely remove the birds from it. Due to this reason, the success of the repellents was determined as a reduction of feral pigeons' use of the experimental shelves by not less than 100%.

Based on the claim of the contact gel distributor, complete avoidance of the prepared shelves was to be expected within seven days of gel application. We therefore categorized three trial phases: pretrial (three recorded days), trial Days 1–7 (five recorded days) when full effectiveness was not yet expected and trial Days 8–26 (11 recorded days) when complete effectiveness was anticipated.

For the visual gel we similarly analyzed the number of approaches and landings, together with the time spent on the shelves. The distributor of the visual gel claimed that the product would be absolutely effective within three days of product application. We characterized three trial phases: pretrial (three recorded days), trial Days 1–3 (two recorded days) and trial Days 4–25 (13 recorded days). Additionally, we distinguished between different behaviors of the pigeon towards the visual repellent: (a) approach without landing and therefore no possible contact, (b) landing with immediate gel contact, (c) subsequent gel contact, and (d) no contact with the gel. We combined the data from the two shelves with the same repellent due to the vicinity of the shelves.

The statistical tests were carried out with the open source statistical package R (R Version 2.15.1 and for the residual analyses R Version 3.0.1 for Mac).

The number of approaches per day for both gels was analyzed using a Quasi-Poisson model (function glm) with phase (three levels as described above) as the sole explanatory factor. Quasi-Poisson was used to account for overdispersion of the data. To model the time spent on the shelves per landing for each gel, we used a linear mixed model (function lmer) with the log-transformed time spent on the shelves as the outcome variable, phase as fixed factor and day as random factor. As uncertainty intervals we calculated Bayesian 95% credible intervals based on 5,000 simulations from the posterior distribution for both number of approaches and time spent on the shelves. Residual analyses included visual inspection of residual versus fitted values plots, quantile-quantile plots for both random effects and fixed effects residuals, as well as temporal autocorrelation plots. These plots indicated no serious violation of model assumptions and no substantial autocorrelation. We use the term "significant" for a fixed effect when the fitted value of one level is not included in the 95% credible interval of the other level.

Moreover, except for the approach without landing, we subdivided the possible behaviors relating to the contact of the landing pigeon with the visual gel (immediate contact, subsequent contact or no contact) into two time based categories: time spent on the experimental shelf ≤3 seconds, or >3 seconds. As pigeons have short reaction times of less than half a second, even in multi-option experiments [25], the 3 seconds that were set as the time to react to the repellents were generously determined and in favor of the effectiveness of the gels. Due to the fact that the complete repellent effect of the visual gel is supposed to have developed two or three days after gel application, we only included trial Days 4–25 in the evaluation of the affected senses. The distributor stated that the optical gel would influence the behavior of the pigeons by affecting not only the visual sense of the birds, but also the senses of smell, touch and taste. We therefore categorized the behaviors of the pigeons into seven classes to determine the affected sense in case of a positive repellent effect. We set the distant visual sense as being influenced when a pigeon approached the shelves but did not land on them. Stimulus of the near visual sense was given if the pigeon left within ≤3 seconds after it had landed on the experimental shelf and showed immediate or no contact with the gel. We defined no visual repellent effect if the pigeon landed first and had subsequent contact with the gel. For the olfactory sense we also set 3 seconds as the time between contact and flying away as the limit for a successful repellent effect, except for the subsequent contact category. Here we defined the inefficacy of the olfactory repellent effect if a pigeon landed on the shelf first and stepped into the gel afterwards. We defined a failure of the system in a tactile sense if the pigeon stood for >3 seconds in the gel. Due to the rare occurrence of events in these categories, a statistical analysis of these data was not appropriate but results were compiled in Table 1.

In terms of the animal welfare point of view we observed the consequences of the pigeons having direct contact with the gels. In addition, the effect of the gel remains transferred to other structures in the loft, and possibly also outside the loft, was described with the potential consequences for other birds.

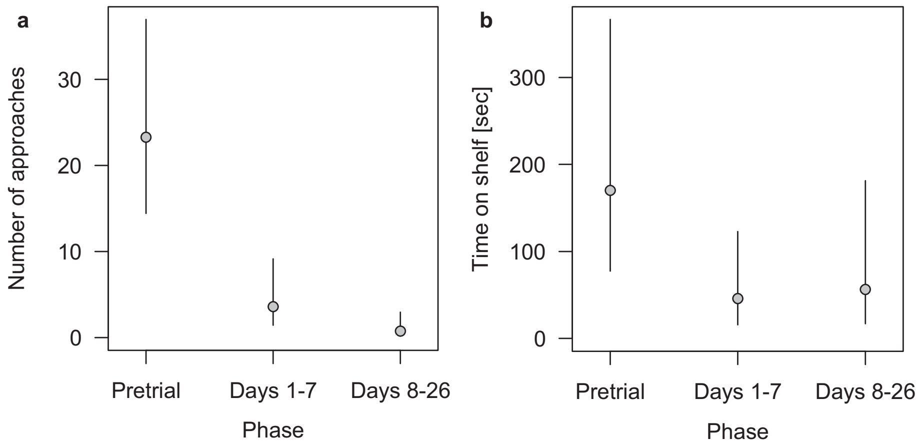
3. Results

3.1. Contact Gel

Figure 1(a,b) shows the results of the contact gel experiment. The numbers of pigeon approaches to the shelves differed by phases. The highest number occurred to the shelves without repellent gel during the pretrial phase (70 approaches). We noted less approaches throughout trial Days 1–7 (18 approaches) and the least during trial Days 8–26 (eight approaches). During the pretrial phase, a mean of 23.3

approaches per day (14.4–37.0 Bayesian 95% credible interval), during trial Days 1–7 a mean of 3.6 (1.4–9.2) and during trial Days 8–26 a mean of 0.75 (0.18–2.95) approaches per day were recorded. The time spent on the experimental shelves during pretrial phase was significantly (or near significantly) longer than during both of the trial phases, but no significant difference occurred between trial Days 1–7 and 8–26 (Figure 1b). During the pretrial phase, the pigeons spent a mean time of 170 (77–367) seconds per landing on the shelf. Trial Days 1–7 showed a mean of 46 (16–123) seconds and trial Days 8–26 a mean of 56 (17–181) seconds per landing. Moreover, we observed only one approach during the pretrial phase that did not lead to a final landing. At this occasion the pigeon flew in the direction of an experimental shelf but turned away shortly before reaching it. In contrast, during trial phase all approaches led to a landing.

Figure 1. Feral pigeons' (**a**) mean number of approaches per day and (**b**) mean time spent on the shelf in seconds per approach for the three phases pretrial, Days 1–7 and Days 8–26 of the contact gel experiment in Basel, Switzerland, during August–October 2012. Values are means and the segments indicate Bayesian 95% credible intervals. For the mean number of approaches, with n per phase being 3, 5 and 11 recorded days, respectively, a Quasi-Poisson model was used. For the mean time spent on the shelf a mixed model with the log-transformed time on the shelf as the outcome variable (results back transformed for the graph) phase as fixed factor, and day as random factor was used with n per phase being 70, 18 and 8, respectively.

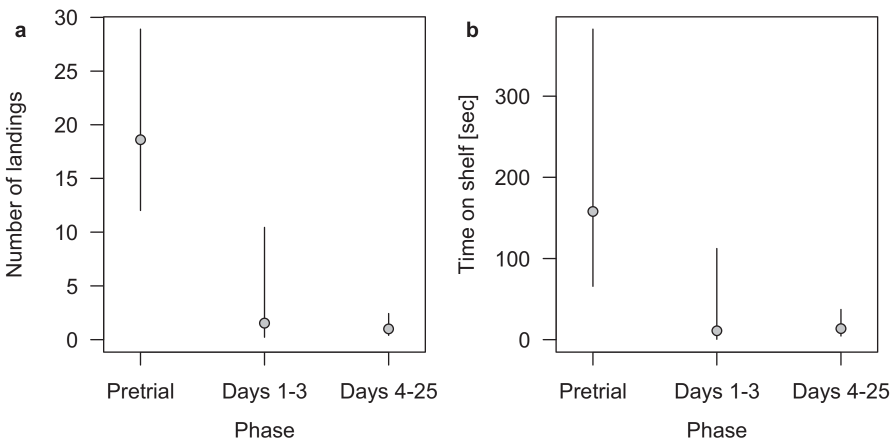


3.2. Optical Gel

During the optical gel repellent test we observed that all approaches to the experimental setup were finished with a landing. We observed a total of 56 landings during the pretrial phase. For trial Days 1–3 we monitored a total of three landings and for trial Days 4–25 a total of 13 landings. The trial phase showed a significant decrease in landings per day compared to the pretrial phase (Figure 2a). During the pretrial phase we detected a mean of 18.6 (12.0–28.9) landings per day, during trial Days 1–3 a mean of 1.53 (0.23–10.45), and during trial Days 4–25 a mean of 1.01 (0.40–2.44). We recorded no difference between trial Days 1–3 and 4–25.

Figure 2b shows that during the pretrial phase, when the shelves were not prepared with the optical gel, the pigeons spent significantly more time on the shelves per pigeon landing than during the trial phases. We observed a mean time spent on the shelves per landing of 158 (66–383) seconds during the pretrial phase, a mean of 11 (0.4–112) seconds for trial Days 1–3 and a mean of 14 (4.5–37) seconds for trial Days 4–25. There was no significant difference between the two trial phases.

Figure 2. Feral pigeons' (**a**) mean number of landings per day and (**b**) mean time spent on the shelf in seconds per landing for the three phases pretrial, Days 1–3 and Days 4–25 of the optical gel experiment in Basel, Switzerland, during August–October 2012. Values are means and the segments indicate Bayesian 95% credible intervals. For the mean number of landings, with n per phase being 3, 2 and 13 recorded days, respectively, a Quasi-Poisson model was used. For the mean time spent on the shelf, a mixed model with the log-transformed time on the shelf as the outcome variable (results back transformed for the graph), phase as fixed factor, and day as random factor was used with n per phase being 56, 3 and 13, respectively.



We summarized the behaviors of the pigeons to the optical gel during trial days 4–25 into seven categories to analyze which sense could have been influenced by the aversive signal (Table 1). All observed 13 approaches led to a landing and all of the stays on the protected shelves lasted >3 seconds.

Table 1. Number of behavioral responses of feral pigeons to the tested optical gel on trial Days 4–25 with determination of the senses appealed to in Basel, Switzerland, during August–October 2012. *f*, far; *p*, possible.

Behavioral response	***n***	**Appealed senses**
Approach without landing	0	Visual (*f*)
Landing, immediate contact, ≤3 sec	0	Visual, tactile, olfactory
Landing, immediate contact, >3 sec	7	No visual, no tactile, no olfactory
Landing, subsequent contact, ≤3sec	0	No visual, tactile (*p*), no olfactory
Landing, subsequent contact, >3 sec	4	No visual, no tactile, no olfactory,
Landing, no contact, ≤3 sec	0	Visual, olfactory
Landing, no contact, >3 sec	2	No visual, no olfactory

When testing the emission of the optical gel, a maximum at 357 nm was found. This demonstrates that the product did emit in the ultraviolet light range, which covers wavelengths of 100 nm until 380 nm.

As to the animal welfare point of view we could observe several pigeons stepping into the gels, either directly when landing onto the experimental shelves or subsequently after landing next to the shelves. Already after a short period of time, both gels looked rather unesthetic and messy due to a variety of insects, feathers and dirt that become stuck in the repellents either directly or in the remains on the shelves (Figure 3).

Figure 3. Appearance of the tactile gel (**a**) and the optical gel (**b**) after 23 days of application. Due to the adhesive effect numerous insects, feathers, dust and feces became stuck in the gels. The gluey optical gel got stuck on the wall underneath the experimental shelf when the pigeons stepped into the repellent and flew off pulling long adhesive strings. These remains were extremely difficult to remove.

While the tactile gel is rather harmless to pigeons regarding its stickiness, the optical gel is of extremely adhesive texture. Here, the possibility of gluing of plumage is definitely given. In addition, it was observed that birds transferred the gels, especially the optical one, to numerous other structures into the loft. Due to the extremely gluey structure of the optical gel, the birds pulled long strings when they stepped into the gel and flew off (Figure 3b). These strings got stuck not only to the experimental shelves, but also to the walls, the ground and were transferred to divers other areas in the loft, as for example the nesting boxes. We can not ensure that the gel was being transferred to other areas outside the loft, but this option seems likely when looking at the numerous traces of gel being spread all over the loft. When cleaning the loft, it was extremely difficult to entirely remove the gel remains. Even strong cleaning agents were used, but some adhesive residues could not be completely removed.

4. Discussion

Both gels showed a restricted repellent effect by reducing the number of approaches of feral pigeons and their time spent on the experimental shelves per landing, but the claimed complete effectiveness, meaning a reduction of the number of birds using the protected structures by 100%, was not observed.

4.1. Contact Gel

The number of approaches during the contact gel experiment decreased constantly over the trial phases. The time spent on the shelves decreased initially, but increased again slightly during trial Days 8–26. We suspect this could be due to initiating habituation. The chance of new birds entering the loft was very low. Techniques such as tactile repellents are recognized to be of limited use because the learned avoidance of the unpleasant sensation extinguishes rapidly [11]. The repellent mechanism of the product tested is supposedly based on a slight irritation of the birds by means of capsaicin, the pungent element of red pepper. While capsaicin is an extremely effective irritant for mammals, birds are almost totally insensitive to it [13,15,16,26,27]. For this reason, a claimed sensory reaction to the gel, as stated by the distributor, is not expected. Instead, we attribute the observed repellent effect as a result of neophobia and discomfort. No complete avoidance of the experimental shelves was observed after a week of gel application. The pigeons rather appeared to get used to the new substance. They often flew onto the treated surface and stood in the repellent, which led to a constant removal of the gel (Figure 3a). Due to this contact with the gel, feces, dirt and feathers were regularly transferred onto the experimental shelves, masking any tactile effect. In addition, numerous insects also became stuck in the gel. Even though the sticky effect of the tactile repellent did not appear to be dangerous for the pigeons, any adhesive effect would make the gluing of plumage possible [12] and therefore contradicts animal welfare. When the birds preen themselves, they possibly disperse the gel even further over and into their plumage. The gel can also be transferred onto other structures and potentially affect non-target, perchance even protected, species.

A repellent effect was detected, but a complete effectiveness of the gel, which is necessary in feral pigeon proofing, is missing. Additionally, the gel has an unpleasant esthetic aspect and a limited life span due to fouling with dust, insects, feathers and feces. Furthermore, the possibility of gluing of plumage and of affecting other structures and non-target birds is given. Due to these reasons, we cannot recommend the tested tactile gel repellent.

4.2. Optical Gel

The optical gel repellent led to a decrease in landings over the trial phases. The time spent on the experimental shelves per landing was initially reduced but then increased again slightly during trial Days 4–25. The gel failed to achieve complete effectiveness since the pigeons still flew onto the treated surfaces after more than 3 days of gel application. According to the distributor, the product tested is able to repel birds visually because it is perceived as fire in their ultraviolet visual spectrum. In addition, the distributor claimed a reinforced repellent effect caused by natural oils that should be abhorrent on an olfactory, gustatory and tactile basis. Even though the effectiveness of certain repellents can be improved by additional sensory cues [28], this gel did not achieve complete avoidance of the perch area after three days of application and thus failed to prove the essential full effectiveness. According to the distributer's statement, the gel is seen as fire by the birds. Despite the fact that pigeons are certainly sensitive to ultraviolet light [29] and therefore could possibly perceive the gel as fire, one wonders how a pigeon should be familiar with fire and associate it with danger given the lack of experience. An inborn avoidance of ultraviolet light and fire lacks any evidence. The emission measurement of the optical gel showed that the gel did emit in the ultraviolet light range. However, only flames at temperatures hotter than 2,500 °C contain ultraviolet parts of the light spectrum. A normal fire by contrast does not contain ultraviolet light [30]. The reasoning of the birds seeing the optical gel as fire could therefore not be reconstructed. In addition, the effect of an outdoor use of the gel in the dark, as well as an indoor use without a supplementary artificial light source, remains questionable. According to our tests, it is not possible that the optical gel owns a repellent effect due to ultraviolet light emission. We suggest instead that the observed change in landings and time spent on the experimental shelves is due to other factors.

Furthermore, we observed a unique event during which a pigeon landed directly into one of the dishes and pecked into the gel repellent after about two seconds. This was repeated twice 13 seconds later. This observation suggests that the gel has no negative effect on the gustatory sense of a pigeon. In addition, all of the 13 approaches led to a landing and the pigeons stood longer than three seconds on the protected shelves or even directly in the gel. This further suggests that the gel does not work on the above-mentioned senses of pigeons.

5. Conclusions

Overall, we conclude that both gels showed a repellent effect, but failed to display the complete effectiveness that is unquestionably essential for a successful feral pigeon management. Our results indicate that capsaicin is ineffective in feral pigeon repellent systems. This is consistent with several other studies and the fact that pigeons are not irritated by capsaicin due to their lack of capsaicin-receptors [13,15,16,26,27]. The primarily observed repulsive effect of both gels is presumably due to neophobia, discomfort and the reduction of space on the shelves. For our second trial phase, we observed a slight, yet statistically not significant, increase in the time spent on the shelves per landing for both gels. Such a fading effect of the repellent is most likely to occur if this effect is based on startle responses due to neophobia. If the relevant stimuli are presented more than a few times, the animals desired to be repelled get accustomed to them [13,31].

As previously shown [19], young and inexperienced birds in particular landed repeatedly on the protected structures. Thus a test run was cancelled prematurely because the chance of nestlings getting directly into contact with the gels was too high. Especially the optical gel had an extreme adhesive effect, which could possibly lead to severe gluing of plumage of any bird as it already occurred with other so-called safe bird repellents [32]. Even weeks after the end of the study, we detected sticky remains of the repellents in the loft. This would definitely leave negative esthetic residues on surfaces if applied onto building facades, possibly causing even more damage than the pigeon droppings themselves. Given the possibility of young birds and also non-target birds coming into contact with the adhesive gels and the fact that any stickiness, even if relatively harmless, contradicts animal welfare, we can not approve the gels.

In our experimental situation, the treated shelves were not particularly attractive to the birds because the pigeon loft offered enough room where the repellents could be avoided. The fact that the pigeons still landed on the treated surfaces shows that even pigeons with low motivation can easily surmount the tested repellents. Summarizing, both gels seem to have only an ineffective, non-permanent repellent effect. Nevertheless, only repellents reducing the number of birds using the treated structures by 100% are effective systems. Therefore the tested products are not recommendable for a successful feral pigeon management.

Systems based on exclusion and mechanical barriers still remain the most reliable repellents. However, the best way of efficiently coping with the pigeon problem in our cities seems to be the reduction of the pigeon population, and this can only be achieved by reducing the food supply of the birds [2].

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Conflicts of Interest

The authors declare no conflict of interest.

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Chapter 3

Taubenabwehr und Tierschutz

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Haag-Wackernagel, D., **Stock, B.** (2015) Taubenabwehr und Tierschutz. In: *Schmerzen, Leiden und Schäden - erkennen, messen und bewerten*, 14. Internationale Fachtagung zu Fragen von Verhaltenskunde und Tierhaltung der DVG-Fachgruppe Ethologie und Tierhaltung; 20. Internationale Fachtagung zum Thema Tierschutz der DVG-Fachgruppe Tierschutz (ed. M. Erhard, A.-C. Wöhr), München, 19.–21. März 2015, DVG Service, Gießen, Germany, pp. 194–207.

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TAUBENABWEHR UND TIERSCHUTZ

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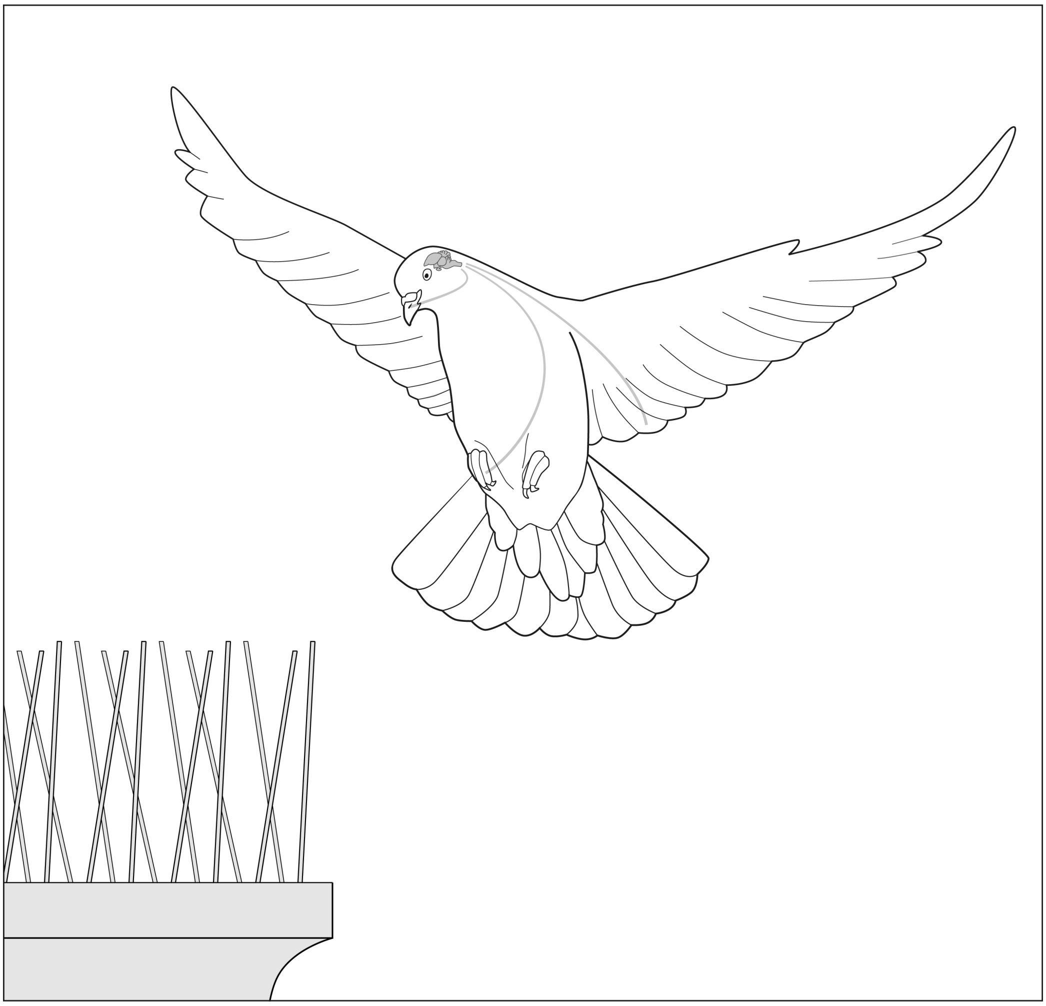

Illustration Nora Gamper

Einleitung

Mit einem Weltbestand von mehreren hundert Millionen Individuen gehört die Straßentaube (*Columba livia* Gmelin 1789) zu den erfolgreichsten synanthropen Vogelarten. Straßentauben sind die frei lebenden Nachkommen von Haustauben und Feldtauben, die ursprünglich von der Felsentaube abstammen. Die frei lebenden Straßentaubenpopulationen sind seit ihrer Verwilderung, die Jahrhunderte zurückliegen kann, wieder denselben natürlichen Auslesemechanismen wie jede andere wild lebende Tierart ausgesetzt. Sie sind deshalb aus biologischer Sicht als Wildtiere zu betrachten, die sich an den Lebensraum Stadt angepasst haben (Köhler 2008).

Die Populationsgröße der Straßentaube wird hauptsächlich durch den Umfang des Nahrungsangebotes bestimmt (Haag 1984). Dank ihrer enormen Anpassungsfähigkeit und einem breiten Nahrungsangebot konnten sich daher in den meisten europäischen Städten große Bestände entwickeln, welche zu verschiedenen Problemen führen können.

Verschmutzungen mit Taubenkot können zu ästhetischen und geruchlichen Beeinträchtigungen sowie zu Materialschäden führen (Haag-Wackernagel 2012a). Reduzenten, welche sonst totes organisches Material abbauen, können in Gebäude eindringen und als Material- und Vorratsschädlinge Probleme verursachen (Haag-Wackernagel 2012b). Aus den Nestern können Ektoparasiten auswandern und den Menschen und seine Haustiere befallen (Haag-Wackernagel und Bircher 2010). Straßentauben sind zudem Reservoir für eine große Zahl von Krankheitserregern, welche auf den Menschen und seine Haustiere übertragen werden können (Haag-Wackernagel 2006). Primär leiden die Straßentauben aber vor allem selbst unter ihrer hohen Dichte, welche sich in Slumbedingungen, wie intraspezifischem Stress, Krankheiten und Parasiten manifestieren (Haag 1991).

Für Hauseigentümer sind es vor allem die Verschmutzungen mit Taubenkot, welche zu Unannehmlichkeiten und zu hohen Reinigungskosten führen können. Es ist deshalb nachvollziehbar, dass diese versuchen Straßentauben mit Taubenschutzmaßnahmen von ihren Gebäuden zu vertreiben und nachhaltig fern zu halten. Unter Taubenschutzmaßnahmen verstehen wir hier bauliche Strukturen oder Veränderungen an bereits bestehenden Gebäuden, welche dazu dienen den Tauben den Zugang und die Nutzung von Gebäudestrukturen zu verhindern. Dazu gehören einerseits bauliche Maßnahmen und andererseits speziell gegen die Tiere gerichtete Taubenabwehrsysteme (Haag-Wackernagel und Geigenfeind 2008, Haag-Wackernagel 2012a). Straßentauben besitzen dank irreversibler Prägungen eine starke Bindung an ihren Brutplatz und ihren Partner. Das bedeutet, dass die Tiere außerordentlich hartnäckig versuchen können, ihre Brutplätze wieder zu erreichen, wenn sie davon ausgeschlossen werden. Es ist deshalb weit schwieriger, ein bereits von Tauben befallenes Gebäude nachträglich zu schützen, als die erstmalige Besiedlung bei einem Neubau zu verhindern (Haag-Wackernagel und Geigenfeind 2008). Taubenschutzmaßnahmen lösen aber keine Probleme, sondern verlagern diese zumeist nur von dem einen auf das nächste Gebäude. Das so genannte Taubenproblem, verstanden als die Folge einer zu hohen Taubenpopulation, kann nur als gesamtstädtische Maßnahme, z.B. durch eine Senkung der ökologischen Kapazität, nachhaltig gelöst werden (Haag-Wackernagel 2003, 2012c).

Während bauliche Maßnahmen, wie z.B. das Verschließen von Einflügen oder die Abschrägung von Fenstersimsen, keine tierschutzrelevanten Probleme verursachen (Haag-Wackernagel und Geigenfeind 2008), stellt sich die Situation bei den Taubenabwehrsystemen komplexer dar. In einer früheren Untersuchung konnten wir belegen, dass brutale Taubenabwehrsysteme, welche den Tieren absichtlich Schäden und Schmerzen zufügen, keine bessere Abwehrwirkung zeigen als harmlose (Haag-Wackernagel 2010). Es ist einzig und alleine die Motivation der Taube, die darüber entscheidet, ob sie eine mit einem bestimmten Abwehrsystem geschützte Struktur zu überwinden versucht oder nicht. Aus diesem Grund muss mit berücksichtigt werden, mit welcher Motivationsstärke die Tauben voraussichtlich ein Abwehrsystem zu überwinden versuchen (Haag-Wackernagel 2010, 2012a). Tauben, welche Eier bebrüten oder Nestlinge betreuen, lassen sich z.B. auch nicht von Spikes mit geschliffenen Spitzen davon abhalten ihr Nest zu erreichen. Stattdessen ist mit einer mittelhohen Motivation der Tauben zu rechnen, den gewohnten Schlafplatz trotz Taubenabwehrsystem zu erreichen, da geeignete, geschützte Schlafplätze in den meisten Städten selten sind. Strukturen wie Aussichts-, Beobachtungs- oder Ruheplätze sind in Form von Dächern, Simsen oder Bäumen meist in genügender Anzahl vorhanden und können durch die meisten Abwehrsysteme einfach geschützt werden, weil die Tauben Ausweichmöglichkeiten besitzen. Im Folgenden werden die rechtliche Situation der Taubenabwehr in Deutschland erläutert und die wichtigsten Taubenabwehrsysteme vorgestellt und bezüglich ihrer Tierschutzgerechtigkeit diskutiert.

Die rechtliche Situation in Deutschland

Straßentauben gingen ursprünglich aus entflogenen Haustauben hervor, die wiederum von den wild lebenden Felsentauben abstammen (Haag-Wackernagel 1998). Aus rechtlicher Sicht werden Straßentauben in Deutschland nicht, wie z.B. in der Schweiz, den Wildtieren, sondern den verwilderten und herrenlosen Haustieren zugeordnet, die nicht dem Jagdrecht unterliegen. Diese Zuordnung ist umstritten, da Straßentauben, die sich teilweise über hunderte von Generationen an das Stadtleben anpassen konnten, nicht mit einem entflogenen Wellensittich verglichen werden können (Köhler 2008). Straßentauben zählen in Deutschland zu den Wirbeltieren ohne besonderen Schutzstatus. Aus diesem Grund werden sie ausschließlich durch das Tierschutzgesetz geschützt.

Bei der Verwendung von Taubenabwehrsystemen sind demzufolge zwei Paragraphen des Tierschutzgesetzes (TierSchG) besonders hervor zu heben. Während § 1 des TierSchG zunächst generell umfassend besagt, dass niemand einem Tier ohne vernünftigen Grund Schmerzen, Leiden oder Schäden zufügen darf, wird unter § 13 Abs. 1 die Verwendung von Abwehrsystemen ergänzend genauer definiert. Dieser Absatz des TierSchG verbietet zum Fangen, Fernhalten oder Verscheuchen von Wirbeltieren Vorrichtungen oder Stoffe anzuwenden, wenn damit die Gefahr vermeidbarer Schmerzen, Leiden oder Schäden für Wirbeltiere verbunden ist.

Laut der Publikation „Tierschutzaspekte bei der Installierung von Taubenabwehrsystemen" des Bundesinstituts für gesundheitlichen Verbraucherschutz und Veterinärmedizin (BgVV) von 2002 ist daher vor dem Einsatz von Taubenabwehrsystemen zu klären, ob durch das System selbst oder aber Art und Zeitpunkt seiner Anbringung negative Auswirkungen auf Tauben, aber auch auf andere Tierarten zu befürchten sind. Das BgVV erläutert in seiner Publikation welche Fragen bei der Installation von Taubenabwehrsystemen im Vordergrund stehen:

Besteht nach Art des Systems die Gefahr, dass:
- sich Tiere am Taubenabwehrsystem verletzen können?
- das Taubenabwehrsystem zu Schäden oder Spätschäden führt?
- das Taubenabwehrsystem zu vermeidbaren Schmerzen oder übermäßigen Schreckreaktionen führt?

Besteht nach Art oder Zeitpunkt der Anbringung des Systems die Gefahr, dass:
- Elterntiere von ihren noch versorgungsbedürftigen Jungen abgeschnitten werden?
- Tiere durch das Anbringen der Absperrung gefangengenommen werden?
- Tiere, welche die Abwehrvorrichtung überwunden haben, den Rückweg nicht finden oder die Abwehrvorrichtung in umgekehrter Richtung nicht überwinden können?

Nur Systeme, bei denen solche negativen Auswirkungen verneint werden können, entsprechen laut BgVV aus tierschutzfachlicher und rechtlicher Sicht den Anforderungen.
In einer Studie konnten wir außerdem zeigen, dass alleine die Motivation von Straßentauben entscheidend ist, ob ein Abwehrsystem überwunden wird oder nicht (Haag-Wackernagel 2010). Die Tiere nahmen bei unserer Untersuchung auch massive Beeinträchtigungen und Verletzungen in Kauf, wobei nozizeptiv wirkende Systeme keinesfalls einen besseren Abwehreffekt erreichten als

harmlose. Abwehrsysteme, die den Tieren Schmerzen, Leiden oder Schäden zufügen, sind daher nicht nur aus rechtlicher Sicht verboten, sondern sie sind auch wissenschaftlich bestätigt nicht effektiver als harmlose Systeme.

Der Markt bringt immer wieder innovative oder überarbeitete Taubenabwehrsysteme hervor. In den meisten Fällen ist es zunächst schwierig einzuschätzen, ob solche Systeme gegen das Tierschutzgesetz verstoßen. Ihre vermeintliche Harmlosigkeit erweist sich oft erst in der Praxis als nicht gegeben. Hierbei werden nicht nur die Tiere einem unnötigen Risiko ausgesetzt, sondern auch der Verbraucher begibt sich auf rechtliches Glatteis. Mangels rechtlicher Grundlagen werden neu entwickelte Abwehrsysteme ohne fundierte wissenschaftliche Überprüfung ihrer Wirksamkeit und ihrer tierschutzrechtlichen Relevanz auf den Markt gebracht. Die Erprobung im Feld wird dadurch dem Anwender überlassen (Haag-Wackernagel und Stock 2014). Aufgrund von mangelnden Verkaufserfolgen und Reklamationen werden solche Systeme dann entweder vom Markt genommen oder, wenn diese ausbleiben, weiterhin produziert.

Wir möchten hier die Bedeutung der wissenschaftlichen Prüfung von Taubenabwehrsystemen vorstellen und die gängigsten Systeme unter Berücksichtigung der rechtlichen und wissenschaftlichen Hintergründe diskutieren.

Beurteilung der Taubenabwehrsysteme

Das ideale Taubenabwehrsystem ist kostengünstig, optisch unauffällig, wirksam, dauerhaft und harmlos für Mensch und Tier. An entsprechenden Anpreisungen der Erzeuger von Abwehrsystemen mangelt es nicht, tatsächlich konnte jedoch bis heute kein solches Idealabwehrsystem entwickelt werden. Generell lässt sich festhalten, dass sich Straßentauben als intelligente und anpassungsfähige Tiere nicht so einfach von ihren existentiell wichtigen Strukturen in der Stadt vertreiben lassen.

Taubenabwehrsysteme lassen sich aufgrund ihrer physikalischen und chemischen Eigenschaften in verschiedene Gruppen einteilen (Haag-Wackernagel 2010). Systeme, welche ihre Wirksamkeit entfalten bevor es zum direkten Kontakt mit den Tauben kommt, werden als Distanzsysteme bezeichnet. Damit sind Systeme gemeint, mit denen die zu vergrämenden Tauben nicht direkt in Kontakt kommen und denen auf Distanz eine wirksame visuelle, akustische oder magnetische Abwehrwirkung zugeschrieben wird. Alle bisher entwickelten Systeme dieser Art haben sich in der Praxis als unwirksam erwiesen. In den Empfehlungen des Australian Transport Safety Bureau (ATSB 2004) werden deshalb Lärm, Mikrowellen, Laser, Ultraschall, Infraschall, Magnetsysteme, Rauch und Lichter als unwirksam bewertet. Obwohl von Ultraschallsystemen (auch Schalldrucksysteme genannt) behauptet wird, dass die Tauben bei Bestrahlung eine unangenehmes Gefühl im Gefieder wahrnehmen sollen, konnten Jenni-Eiermann et al. (2014) aufgrund von Messungen des Kortikosterons und von Verhaltensbeobachtungen solche Effekte ausschließen. Geruchsabwehrsysteme auf der Basis von chemischen Abwehrstoffen, sogenannten Repellentien, haben sich ebenfalls als unwirksam erwiesen (Haag-Wackernagel 2010). Da alle bekannten Distanzabwehrsysteme weder Wirkung auf die Tauben zeigen noch diesen nachweislich Schäden zufügen können, sind sie nicht tierschutzrelevant und werden im Folgenden nicht weiter berücksichtigt.

Abwehrsysteme, welche eine negative Interaktion mit Körperkontakt beabsichtigen, werden als Kontaktabwehrsysteme bezeichnet. Dabei ergeben sich fließende Übergänge, da die meisten Abwehrsysteme, mit Ausnahme der olfaktorischen Abwehrmethoden, auch visuelle Eigenschaften aufweisen und deshalb einen optischen Abwehreffekt ausüben können. Tabelle 1 umfasst die wichtigsten Taubenabwehrmethoden mit ihren Eigenschaften und ihrer tierschutzrechtlichen Relevanz. Problematische Taubenabwehrsysteme werden weiter unten detailliert diskutiert.

Tabelle 1: Die wichtigsten handelsüblichen Kontakt-Taubenabwehrsysteme und deren tierschutzrechtliche Beurteilung

Abwehrmethode	Beschreibung	Vorteile/Nachteile	tierschutzrechtliche Beurteilung
Vogelnetze	Monofile oder polyfile Polyethylen-Netze, vertikal oder horizontal gespannt, meist an Randseilverspannung fixiert	gute Abwehrwirkung, langlebig, optisch unauffällig, anspruchsvolle Montage, erfordert Verankerung in der Bausubstanz, Wartung notwendig	bei korrekter Anwendung harmlos, problematisch, wenn Tauben durch mangelhafte Montage oder fehlende Wartung hinter Netze gelangen
Vergitterungen	Gitter aus Edelstahl, mit Rahmen fixiert	gute Abwehrwirkung, langlebig, optisch auffälliger als Netze	bei korrekter Anbringung unproblematisch
Elektroschock-systeme	Stromstoßgenerator mit Stangen, Drähten oder flachen Bändern (Viehhüterprinzip)	gute Abwehrwirkung, unauffällig, Warnhinweise wegen Stromschlag, Wartung notwendig	problematisch bei zu hoher Leistung, Widerstandsregelung empfehlenswert, schwacher optischer Abwehreffekt
Metallspikes geschliffen	geschliffene Metallspitzen	mittlere Abwehrwirkung, langlebig, Verletzungsgefahr bei der Montage, optisch auffällig, Abfallsammler	nicht tierschutzgerecht, Verletzungsgefahr
Metallspikes stumpf	stumpfe Spitzen, 1–2 mm Durchmesser, häufigstes Abwehrsystem	mittlere Abwehrwirkung, langlebig, optisch auffällig, Abfallsammler	harmlos, trotz gegenteiliger Behauptung keine Verletzungsgefahr
Kunststoffspikes	stumpfe Spitzen	mittlere Abwehrwirkung, optisch auffällig, kurzlebig, Abfallsammler	harmlos
Spanndraht	dünne Edelstahlseile (ca. 0,5 mm Durchmesser) mit Spannfedern, auf Haltern	schwache Abwehrwirkung, optisch unauffällig	relativ harmlos, bei nicht mit Kunststoff ummantelten Seilen Verletzungsgefahr
Abwehrgele	Dauerelastische Pasten, teilw. kombiniert mit Abwehrgerüchen und optischen Abwehreffekten	schwache bis fehlende Abwehrwirkung, Verschmutzung des Untergrundes	nicht tierschutzgerecht, meist fehlender optischer Abwehreffekt, Gefahr der Verklebung bei Tauben und anderen Vögeln

Problematische Taubenabwehrsysteme

Vogelnetze

Vernetzungen besitzen eine hohe Abwehrleistung und können sehr vielfältig angewendet werden. In fachlich guter Ausführung gehören sie zu den langlebigsten Systemen, die besonders bei Großflächenanwendung kostengünstig und optisch unauffällig sind. Das Netz muss immer straff gespannt sein und darf an keiner Stelle größere Öffnungen als die Maschenweite aufweisen. Eine optimale Spannung kann nicht erreicht werden, wenn ein Netz nur mit Heftklammern am Untergrund befestigt wird.

Tauben können sich auch durch kleinste Lücken zwängen und somit hinter die Netze gelangen. In solchen Fällen finden die Tauben den Ausweg meist nicht mehr oder verfangen sich in Verengungen zwischen Netz und Untergrund (Abb. 1). Wenn Tauben, die hinter ein Netz gelangen zu fliehen versuchen, können sie sich vollständig verheddern (Abb. 2). Werden die Tiere nicht befreit, gehen sie elend zugrunde. Hinter Netzen verfangene Tauben müssen aus Tierschutzgründen z.B. durch die Feuerwehr befreit werden. Die teilweise hohen Kosten gehen zu Lasten der Hauseigentümer. Regelmäßige Wartungen von Vernetzungen können sich deshalb nicht nur aus tierschützerischen Bedenken durchaus lohnen.

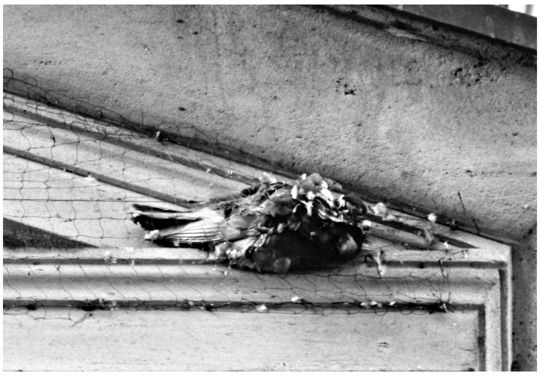

Abbildung 1: Eine Straßentaube gelangte hinter ein Netz welches statt mit einer Rahmenverspannung nur locker mit Ösen befestigt wurde. Bei einem Versuch zu entkommen geriet das Tier zwischen Netz und Hauswand, verhedderte sich und ging elend zugrunde.

Abbildung 2: Die Tauben konnten den hinteren Bereich eines vernetzten Balkons weiter als Brutplatz nutzen. Bei einem Fluchtversuch verfing sich das Tier im Netz und konnte befreit werden. Foto E. Lauber

Elektroschocksysteme

Zurzeit werden verschiedene Typen von Elektroschocksystemen gegen Straßentauben angeboten, welche sich in der Art des Stromträgers unterscheiden (Metallstangen, Drähte, Profilelektrosysteme, Flachprofile). Alle diese Elektroschocksysteme arbeiten nach dem Prinzip eines Viehhüters.

Anforderungen des Tierschutzes an Elektrosysteme gegen Tauben wurden von Schütt-Abraham (2002) formuliert. Um einen Abwehreffekt zu erzielen, müssen die Stromstöße von den Tauben deutlich wahrgenommen werden und eine Schreckreaktion auslösen. Nicht vertretbar sind Ströme, die anhaltende Schmerzen, Verletzungen oder Verbrennungen hervorrufen oder zu Verkrampfungen der Füße führen, die ihnen ein Loslassen und Wegfliegen verunmöglichen. Elektrosysteme müssen deshalb wie Weidezaungeräte mit Einzelimpulsen oder Impulspaketen bei hohen Voltzahlen und geringer Impulsdauer und tiefen Stromstärken arbeiten. Der Abstand der Impulse muss lang genug sein, damit die Tauben fliehen können, bevor der nächste Stromstoß folgt. Bei der Konstruktion von Elektrosystemen ist zu berücksichtigen, dass der Übergangswiderstand zwischen dem elektrischen Leiter und dem Taubenfuß, der die maximale erreichbare Stärke des Impulses im Tier begrenzt, von unterschiedlichen Faktoren abhängt. Der Verhornungsgrad der Fußhaut ist bei jungen Tauben geringer, sodass Jungtauben einen stärkeren Schlag erhalten als Adulttiere. Eine Taube mit nassen Füssen oder einer Verletzung erhält ebenfalls einen stärkeren Stromstoß. Aus Tierschutzgründen muss gefordert werden, dass Elektrosysteme mit einer Vorrichtung ausgerüstet werden, die verhindert, dass die zum Erreichen des Vergrämungseffektes erforderliche Impulsstärke nicht wesentlich überschritten wird. Elektrosysteme ohne eine solche "Tierschutzsicherung" müssen als nicht tierschutzgerecht abgelehnt werden, da sie den Tauben unnötig Schmerzen zufügen.

Elektrosysteme sind auch dann wirksam, wenn sie mit einer Spannung arbeiten, die für die Tauben relativ unbedenklich sind. Diese Grenze dürfte bei etwa 7000 Volt bei 0.1 A bei 10 KΩ Widerstand liegen (Haag-Wackernagel 2010). In den Versuchen bewirkte diese Spannung keine sichtbare Schmerzreaktion. In Deutschland und der Schweiz gibt es zurzeit kein Zulassungsverfahren für Taubenabwehrsyteme und infolgedessen auch keine zugelassenen Vorrichtungen (Schütt-Abraham 2002). Somit muss im Einzelfall geprüft werden, ob das System den jeweiligen Tierschutzgesetzen entspricht und weder bei Tauben noch bei anderen Wirbeltieren vermeidbare Schmerzen, Leiden und Schäden verursacht.

Metallspikes

Metallspikes die auf eine Kunststoff- oder Metallbasis fixiert sind gehören zu den am weitesten verbreiteten Abwehrsystemen, weil sie relativ preiswert und einfach anzubringen sind. Mit den passenden Spikesystemen können alle Fassadenteile, wie Simse, Nischen, Ornamente, Regenrinnen, Schneefanggitter und auch Skulpturen, Photovoltaikanlagen und sonstige Flächen geschützt werden. Bereiche, die zunächst als Nist- und Schlafplätze dienten, sollten gegen erneuten Anflug durch verlässlichere Maßnahmen geschützt werden, da ausgeschlossene Tauben mit hoher Motivation versuchen, die neu installierte Abwehr zu überwinden. Tauben können die Spikes durch Auflage von Nistmaterial unwirksam machen und sogar zur Stabilisierung ihrer Nester verwenden, wenn hinter den Spikesreihen mehr als 10 cm Platz bleibt. Aus der Sicht des Tierschutzes müssen zwei Typen von Metallspikes voneinander unterschieden werden.

A. Metallspikes mit geschliffenen Spitzen

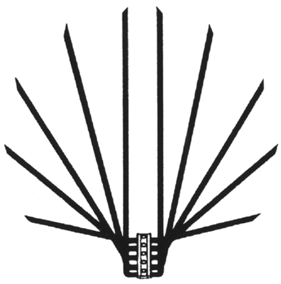

Abbildung 3: Metallspikes mit geschliffenen Spitzen können bei den Tauben wie auch beim Menschen zu Verletzungen führen. Diese Systeme sind nicht tierschutzgerecht.

Abbildung 4: Die abgebildete Taube brütet hinter einem mangelhaft montierten Spikessystem mit scharfen Spitzen, an dem sich die Adulttiere und die Nestlinge verletzen können.

Spikes mit geschliffenen Metallspitzen, wie z.B. Nixalite (http://www.nixalite.com), wurden ursprünglich dazu verwendet Gefangene am Ausbrechen zu hindern, indem es z.B. auf Gefängnismauern montiert wurde. Das System zeigt auf Tauben eine ausgeprägte optische Abwehrwirkung. Trotzdem können sich die Tauben verletzen, wenn sie unter einer hohen Motivation ihren Brutplatz zu erreichen versuchen, die Spikes mit der Brust wegdrücken oder über das System zu laufen. Dabei können sie durch die scharfen Spitzen gestochen werden. In unseren Versuchen zeigte dieses System keine bessere Abwehrwirkung als harmlose Spikessysteme (Haag-Wackernagel 2010). Aus diesem Grund müssen Spikes mit geschliffenen Spitzen als nicht tierschutzgerecht bewertet werden und verstoßen gegen das Tierschutzgesetz.

B. Metallspikes mit stumpfen Spitzen

In Tierschutzkreisen wird immer wieder behauptet, Metallspikes mit stumpfen Spitzen könnten den Tauben ernsthafte Verletzungen zufügen. In unseren Versuchen konnten wir in keinem Fall feststellen, dass sich Tauben an stumpfen Spikes verletzten, auch wenn sie mit sehr hoher Motivation versuchten die Strukturen hinter dem System zu erreichen (Haag-Wackernagel 2010). De Vita (2009, 2010) zeigt dramatische Bilder, in denen dargestellt wird, wie Metallspikes eine Straßentaube vollständig aufspießen und dabei den Brustbeinkamm, die Leber und den Magen durchdringen. Hämorrhagien weisen darauf hin, dass die Taube beim Aufspießen noch gelebt hat. Die massiven Verletzungen setzen einen ungebremsten Sturzflug der Taube direkt auf das Spikessystem voraus, was für eine landende Taube völlig untypisch ist. Wenn eine Taube auf einer Fassadenstruktur landet, bremst sie den Flug stark ab, sodass sie mit einem kleinen Sprung auf der

Oberfläche aufsetzen kann. Die dabei wirkende Kraft würde niemals dazu ausreichen, eine Perforation des Brustbeinkamms zu bewirken. Es bleibt damit der Verdacht, dass die von De Vita (2010) fotografierte Taube absichtlich noch lebend von Unbekannten auf die Spikes gedrückt wurde.

Solche auf Spikessysteme aufgespießte Tauben konnten wir ebenfalls in einem Fall in Basel beobachten. Eine mögliche Erklärung dafür ist, dass gewisse Menschen leider immer noch daran glauben, dass die Beobachtung eines Todeskampfes eines Artgenossen als solcher wahrgenommen wird und so eine abschreckende Wirkung auf unerwünschte Vögel entfaltet. Es versteht sich von selbst, dass solche tierquälerischen Praktiken nicht nur unethisch und strafbar, sondern auch völlig wirkungslos sind. Zumindest Tauben reagieren auf tote Artgenossen völlig gleichgültig und nehmen diese wohl kaum als abschreckend wahr.

Spanndrahtsysteme

Abbildung 5: Spanndrahtsysteme können in seltenen Fällen zu Verletzungen führen, wenn die Drahtseile nicht mit Kunststoff ummantelt sind. Eine Taube verletzte sich hier beim Versuch davon zu fliegen in dem der Draht eine tiefe Schnittwunde verursachte. Foto Dr. Nicolas Späth.

Spanndrahtsysteme sind optisch relativ unauffällig, verfügen aber nur über eine eingeschränkte Wirksamkeit. Das System gilt im Allgemeinen als harmlos für die Tauben. In einem von N. Späth und R. Hufschmid (pers. Mitteilung) dokumentierten Fall hielten sich Tauben zwischen zwei Drähten auf, welche zu weit auseinander lagen. Als ein Täuber auffliegen wollte, verfing sich der Spanndraht oberhalb des Beins. Beim Versuch sich zu befreien, schnitt sich der Draht tief ein und riss danach. Dies führte zu einer so tiefen Wunde (Abb. 5), dass das Tier nicht gerettet werden konnte. Das aus sieben Drähten verdrillte Seil wies einen Durchmesser von 0,45 mm auf und besaß keine PVC-Ummantelung. Diese verhindert die Verletzungsgefahr während der Montage und das Aufspleißen am Ende des feinen Drahtseils. Im Interesse des Tierschutzes, wie auch der Anwender, sollten deshalb nur ummantelte Spanndrähte von mindestens 0,7 mm Durchmesser verwendet werden, bei denen keine Verletzungsgefahr besteht.

Abwehrgele

Die Wirkungen sogenannter Abwehrgele beruhen auf verschiedenen Mechanismen. Neben Kontaktgelen, die den Tauben bei Berührung des Gels eine milde, harmlose Reizung vermitteln sollen, existieren auch optische Gele. Diese sollen ihre Wirkung durch die Emission von Ultraviolettlicht entfalten, welches die Tauben angeblich als Feuer wahrnehmen. In unseren Versuchen konnten wir zwar zunächst eine gewisse Abwehrwirkung beobachten, jedoch war keines der Gele in der Lage die Tauben nachhaltig von den Strukturen fernzuhalten (Stock und Haag-

Wackernagel 2014). Des Weiteren ließ diese begrenzte Schutzwirkung nach einigen Tagen wieder nach, was wahrscheinlich auf das für Tauben übliche zögerliche Verhalten gegenüber ihnen unbekannten Situationen zurück zu führen ist und als Neophobie bezeichnet wird. Neben der unbefriedigenden Abwehrwirkung sind solche Gele auch aus tierschützerischer Sicht abzulehnen. Da sie keine ausreichende optische Abwehr auf die Tauben ausüben, kam es bei unseren Versuchen immer wieder zu verschiedenen Kontakten mit den Gelen. Die Tiere flogen entweder direkt in die Gele hinein, landeten neben diesen und liefen anschließend hinein, oder aber sie pickten sogar in die Gelpasten. Nach Wormuth und Lagoni (1985) können Vergrämungspasten insbesondere bei Kleinvögeln von der Verklebung des Gefieders, des Schnabels und der Extremitäten bis zur Flugunfähigkeit und zum Tod führen.

Während Nistboxversuchen konnten wir keine Reaktion beobachten, welche auf Missbehagen oder eine Schreckreaktion hingewiesen hätte. Stattdessen traten die Tauben immer wieder in die Gele hinein und verschmierten die stark klebende Substanz in den Boxen. Da somit nicht nur die Gesundheit der Adulttiere, sondern auch die der flugunfähigen Nestlinge gefährdet war, mussten wir den Versuch abbrechen. Auch noch nach Wochen konnten wir die schwer zu entfernenden Rückstände der Gele an mehreren Stellen des Versuchsschlages finden. Durch den starken Klebeeffekt kann somit die eigentlich zu schützende Hausfassade äußerst unansehnlich verschmutzt werden, da in den Gelen Federn, Staub, Vogelkot und Insekten haften bleiben. Zudem kann auch nicht garantiert werden, dass nicht noch andere Vogelarten mit den Gelen in Kontakt geraten. Aus tierschützerischen Gründen sollten Abwehrgele, wie schon von Wormuth und Lagoni (1985) und von Fröhlich (2002) vorgeschlagen wurde, nicht angewendet werden, da ihre Wirkung nicht kontrolliert werden kann.

Prüfung von Taubenabwehrsystemen

Tauben können mit Taubenabwehrsystemen unterschiedlicher Wirksamkeit von einzelnen Gebäuden und anderen Strukturen ferngehalten werden. Dabei ist darauf zu achten, dass die Forderungen des Tierschutzgesetzes eingehalten werden. Dieses verbietet zum Fangen, Fernhalten oder Verscheuchen von Wirbeltieren Vorrichtungen oder Stoffe anzuwenden, wenn damit die Gefahr vermeidbarer Schmerzen, Leiden oder Schäden für Wirbeltiere verbunden ist. Diesen Forderungen wird in der Praxis oft nicht entsprochen. Viele Abwehrsysteme werden ohne Überprüfung ihrer Wirkung auf die Tauben und andere Vogelarten bedenkenlos auf den Markt gebracht. Erst im Nachhinein zeigt sich dann, dass die Systeme gegen das Tierschutzgesetz verstoßen.

Problematisch ist hierbei nicht nur die rechtliche Grauzone in der sich der Verbraucher bewegt. Beim Einsatz nicht zuvor getesteter Taubenabwehrsysteme werden zudem die Tiere einer unnötigen Gefährdung ausgesetzt, da brutale Taubenabwehrsysteme, welche den Tieren absichtlich Leiden, Schäden und Schmerzen zufügen keine bessere Abwehrwirkung zeigen als harmlose (Haag-Wackernagel 2010). Systeme die den Tauben schaden, sind daher nicht nur aus rechtlicher Sicht verboten, sondern auch noch wissenschaftlich bestätigt nicht effektiver als harmlose Systeme.

Wir empfehlen daher, dass Taubenabwehrsysteme einem Prüfungsverfahren unterzogen werden bevor sie in den Verkauf gelangen. Bestimmte Taubenabwehrsysteme, wie z.B. Vernetzungen sind bei korrekter Funktion bedenkenlos, hingegen können sie durch mangelhafte Anbringung oder durch altersbedingten Verschleiß zu tierschutzrelevanten Gefährdungen führen. Bei der Beurteilung eines Taubenabwehrsystems ist deshalb auch auf solche sekundären Gefährdungen zu achten, denen durch entsprechende Forderungen nach regelmäßigen Funktionskontrollen und Wartungen begegnet werden kann. Wissenschaftliche Untersuchungen eines jeden Systems auf möglichen Verstoß gegen das Tierschutzgesetz sowie das Verhalten der Tauben den Systemen gegenüber und den sich daraus ergebenden tierschützerischen Konsequenzen sollten von einer neutralen Instanz durchgeführt werden. Idealerweise könnte ein Prüfsiegel tierschutzkonforme Systeme auszeichnen, die den Richtlinien des BgVV bzw. dem Tierschutzgesetz entsprechen. Ein solches Siegel würde nicht nur die Tauben schützen, sondern auch die Verbraucher rechtlich absichern.

Da eine Implementierung eines Prüfungsverfahrens seine Zeit braucht, könnte als Übergangslösung auf empirischer Grundlage und bereits vorhandener wissenschaftlicher Untersuchungen eine Liste mit empfehlenswerten Taubenabwehrsystemen und den Voraussetzungen ihrer Anwendung erarbeitet und veröffentlicht werden.

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Chapter 4

Food shortage affects reproduction of Feral Pigeons *Columba livia* at rearing of nestlings

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Food shortage affects reproduction of Feral Pigeons *Columba livia* at rearing of nestlings

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Feral Pigeons *Columba livia* are highly adapted to urban environments and are thus often abundant in cities. This can lead to various problems, including fouling of building facades and pavements, transmission of allergens and pathogenic micro-organisms, and infestations of ectoparasites derived from breeding sites. To develop effective, long-lasting and humane control strategies, it is necessary to understand the demography of Feral Pigeons. Although food shortage is a major source of reproductive failure in Feral Pigeons, it is still unclear at which phase of the reproductive cycle this reduces overall reproductive success. Here, we assess the effect of a sudden reduction in the food base on the reproduction of a well-studied Feral Pigeon breeding colony. The findings of this study suggest that the number of broods per pair decreases significantly during food scarcity, and that although hatching success remains constant, a significantly greater number of nestlings die during the rearing phase. This suggests that the high energy demand of Feral Pigeon nestlings could not be met under conditions of food scarcity, which reduced the total number of fledged young by more than half and led to a reduction in the colony size. These results have important implications for selecting suitable, durable and humane control strategies for the management of large Feral Pigeon populations in urban environments.

Keywords: breeding biology, food loss, food reduction, nestling mortality, nutrition, population regulation.

INTRODUCTION

Food supply limits reproductive success and survival of both the young and the parents in many bird species (Martin 1987). For example, artificially reduced brood sizes or increased food supply result in a consistent increase in size and survival prospects of the young (Martin 1987).

Feral Pigeons are the free-living descendants of domesticated forms of the wild Rock Dove *Columba livia*. They populate most cities in temperate regions (Baptista *et al.* 1997). The size of Feral Pigeon populations is mainly determined by their food supply. The available food base is intentionally supplied by humans or available as human food waste. The partial absence of effective regulation by predators and the rich food base allow the development and maintenance of large populations that can cause human health problems, including fouling with faeces and transmission of pathogenic micro-organisms and parasites to humans (Haag 1991). Each pigeon produces 4–11 kg of faeces annually (Vogel 1997), soiling breeding areas, house facades, monuments, streets and other city sites. Zucconi *et al.* (2003) estimated the overall damage to be €23.7–33.5 (US$ 27–38) per Feral Pigeon per year. Additionally, 111 pathogenic agents and 20 harmful arthropod species that can infest humans have so far been found in Feral Pigeon populations (Haag-Wackernagel & Moch 2004, Haag-Wackernagel & Bircher 2010). While many wild-living species have a parasitic fauna comparable to that of Feral Pigeons, no other species lives as close to humans and offers so many possibilities of transmission. For all these

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reasons, the Feral Pigeon represents an important study species for which to consider the impact and mechanisms of changing food supply on reproduction.

Estimates of pigeon demographic parameters and their variability are crucial when selecting a suitable control strategy because they provide a working basis for determining the feasibility of deterrence or population control (Giunchi *et al.* 2012). Principal options include the protection of specific buildings or city-wide solutions aimed at the reduction of pigeon populations. However, most interventions either lack scientific proof of efficacy or have failed to prove effective when tested (Stock & Haag-Wackernagel 2014). Furthermore, several studies have demonstrated that culling has no long-lasting effect on the population size, because Feral Pigeons tend to fill the losses quickly through compensatory natality and immigration (Murton *et al.* 1972, Haag 1984, Kautz & Malecki 1990, Sol & Senar 1995, Schnitzler 1999).

Many birds adjust their clutch size to environmental conditions, having smaller clutches when food is scarce and larger clutches when it is abundant. This ability to vary clutch size is one way of allocating reproductive energy (Burley 1980). Another option is to modify the interval between successive clutches, thus creating the possibility in good food conditions of clutch overlap where two successive clutches are being cared for simultaneously (Burley 1980). Feral Pigeons pursue a breeding strategy that aims to achieve the greatest number of broods to produce as many fledglings as possible (Hetmański & Barkowska 2008). Relevant evolutionary strategies include two-egg clutches, small eggs (Robertson 1988), quick replacement of lost clutches (Johnston & Janiga 1995), feeding the nestlings with highly nutritious crop milk (Gillespie *et al.* 2012), overlapping clutches (Burley 1980, Hetmański & Wołk 2005), biparental care of the brood and all-season breeding under optimal feeding conditions (Häkkinen *et al.* 1973, Johnston & Janiga 1995).

The raising of young is time- and energy-consuming for both parents. During the first few days, nestlings are fed exclusively with crop milk. When the squabs grow older, the milk is mixed with soaked grains and is gradually replaced by grains only (Vandeputte-Poma 1980). As a result of being fed highly nutritious crop milk, pigeon squabs have a uniquely high growth rate. There is no parallel among the young of animal species studied so far to the 22-fold increase in body weight in the first three postnatal weeks seen in pigeon squabs (Shetty *et al.* 1992). Biparental feeding of crop milk allows Pigeons to raise their young independently of specific nestling food. The feeding of the quickly developing young, however, comes with an increased energy input and enormous resource requirements for both parents. An adult rearing a 10-day-old nestling consumes 243% of the average daily food intake of a non-incubating single adult (Riddle & Braucher 1934).

Feral Pigeon populations depend heavily on abundant food to pursue these reproductive strategies (Haag 1984). A reduction in food supply leads to increased investment in foraging, which in turn reduces reproductive output, and could reduce population size if neither immigration nor survival rates are able to compensate. While the impact of food limitation on Feral Pigeon populations has already been described (Johnston & Janiga 1995), it is unknown at which phase of the reproductive cycle a food shortage reduces overall reproductive success. In this study we investigated the effect of a reduction in the food base on the reproductive cycle of a well-studied Feral Pigeon breeding flock under natural living conditions over a period of 8 years. We predicted that the number of Feral Pigeon breeding pairs and broods per pair would be limited under food shortage. We also expected the interval between clutches to increase. Additionally, as some species limit their clutch size under less favourable environmental conditions, the number of eggs per brood provides insights into alternative reproductive strategies in adapting to a limited food base. We thus tested whether the number of eggs per clutch and per year was reduced after food limitation took place. Because the Pigeons had to spend more time foraging, we also expected reduced hatching and fledging success. Lastly, we examined whether any change in reproductive output led to an overall change in population size after food limitation. Our overall aim was to define the extent and main drivers of any change in reproduction under conditions of food scarcity. Specialists dealing with pest species depend on such results when choosing the most promising and durable control strategy against an abundant species, such as the Feral Pigeon, and to implement such strategies to achieve an appropriate and humane existence of Feral Pigeon populations in urban environments.

METHODS

Study site

The Feral Pigeon population used for this study occupies a pigeon loft managed by the authors within the framework of the 'Pigeon Action of Basel' (Haag-Wackernagel 1993). The loft is situated in the St Matthew Church in a residential quarter on the outskirts of Basel, Switzerland (47°34′N, 7°35′E). It has a floor space of 28 m^2 and is equipped with 39 breeding boxes, although a few pairs also nest on the floor or on ledges formed by beams and boards. The loft is cleaned of droppings, nesting material and carcasses every alternate week, and breeding data as well as general observations are recorded. The Pigeons use the loft as a roosting and breeding site only. They are free to enter or leave at any time with the exception of nocturnal censuses, during which all Pigeons present are captured and data, as specified below, are recorded. Pigeons hatched in the loft are individually marked with an aluminium leg ring at fledging age, and immigrant birds are ringed during the nocturnal censuses. Every ringed Pigeon has been registered in a database since the opening of the loft. The colony varies seasonally between 75 and 100 individuals. The birds are not fed by the researchers and must search for food and water themselves. Thus, they are exposed to the prevailing urban conditions. In a previous study (Rose *et al.* 2006) we found that the birds foraged mainly within 300–2000 m of the loft, and especially at the Rhine Port St Johann, 1 km away, where large amounts of wasted grain were consistently available. The port management have stated that approximately 60 tons of grain were spilled yearly, most of which was consumed by Feral Pigeons. Assuming a daily intake of 29 g per individual (Haag 1984), this food source alone could feed around 5700 Feral Pigeons throughout the year. Additionally, the birds from the study loft were recorded foraging in local streets and other areas around the loft. At the end of December 2009, the Rhine Port St Johann was closed and demolished. The population thus lost its main food source within a few days. This allowed us a unique opportunity to study the effect of a sudden change in food availability on reproductive success and population dynamics.

Data collection

We recorded reproduction data for active nests every other week for 8 years (November 2005–October 2013). We restricted data recording to a biweekly interval to reduce potential disturbances to a minimum. We collected the following data: number and condition of the eggs (incubated, abandoned or damaged), number, weight and estimated age of the nestlings, based on weight as well as plumage development after Johnston and Janiga (1995), and ring number on ringing. Laying date was defined according to the hatching date of the nestlings, which was calculated through their age based on weight. For abandoned or damaged clutches we assumed the laying date to be 9 days before egg recording, which represents half the incubation time of a successful incubation period of 18 days.

We made eight additional nocturnal breeding colony censuses during the study period. These censuses were necessary to identify all birds in the breeding colony and to determine the size of the colony. During the censuses, we closed the exit holes from the outside to hinder the pigeons from fleeing the loft. We caught all pigeons with hand nets, placed them in boxes and examined them individually. Numbered leg rings identified each bird and unmarked immigrant birds were ringed.

As nesting attempts are difficult to trace back to a definite date, we chose to rely on clutch interval length to draw reliable conclusions on the breeding history of a pair. The interval between successive clutches was defined as the number of days from the date the first egg was laid to the date the first egg of the next clutch was laid (Burley 1980). Clutch intervals were also calculated in cases when the second clutch ended in the loss of eggs or nestlings.

The number of breeding pairs nesting in the colony in a particular year was calculated as the number of nesting sites occupied at least once in that year, following Murton and Clarke (1968). The number of active nests per day was estimated using the data on recorded eggs, nestlings and fledged young. The number of pairs estimated to be breeding at the time of the nocturnal censuses was defined as the number of active nests with eggs or nestlings from 1 week before until 1 week after each nocturnal census.

Hatching success was defined as the ratio of the number of nestlings hatched to the number of eggs laid, and fledging success as the ratio of fledged young to nestlings hatched (Dabert 1987). We had complete nest histories for all nests and thus expected no relevant nest exposure effect in our data because nests that were started and already failed between two of our biweekly intervals would still be recognized because the eggs were still present and were recorded. The mean annual reproductive success (ARS) was therefore calculated by dividing the number of fledged young by the number of breeding pairs in a particular year.

Data analysis

For clutch interval, a normal linear mixed model was fitted with log-transformed clutch interval as the response variable and port closure (before vs. after) as a binary categorical fixed effect. Nest and year were entered as random factors to account for non-independence within the data.

To model the change of the annual total number of nesting attempts, eggs, hatched and fledged young and the number of breeding pairs, we used Poisson models with a log-link to compare the means before and after port closure (one model for each of these five response variables and $n = 8$ for each of these models, as the response variables have one value per year). Models included an observation-level random effect to account for overdispersion. The number of nesting attempts per pair and per year, clutch size, and ARS were also estimated using Poisson models. For these three models, the measurement levels were the breeding pair ($n = 338$, for nesting attempts per pair and ARS) and the individual nesting attempt ($n = 831$, for clutch size), respectively. The factor 'before vs. after port closure' was fitted as a fixed categorical effect. Breeding pair (estimated as birds breeding in the same nest) and year (years from November to October the following year, as this study started in November) were fitted as random effects. There was no indication of overdispersion in these models.

To estimate the probability of hatching per egg (hatching success) and of fledging per hatchling (fledging success), two binomial models with the number of successes and failures were used (with a logit-link function). For both models, the measurement level was the individual brood ($n = 831$ for hatching success and $n = 328$ for fledging success), and the number of successes and failures per brood were the response variable. Again, breeding pair and year were random effects and no strong overdispersion was observed.

Inference from these models used Bayesian 95% credible intervals based on 10 000 samples from the joint posterior distribution (the 95% Bayesian credible interval contains the true parameter value with a probability of 95%, given that the model assumptions are met; flat priors were used with the function sim of the R package arm).

RESULTS

Data from 831 broods collected in 8 years were included in the analysis. From 1429 eggs, 535 nestlings hatched (37.4%) of which 353 successfully fledged (66.0%). Overall ARS was 1.03 fledged young per breeding pair per year. The average number of Pigeons present during the nocturnal censuses was 111 in the years before and 82 in the years after port closure, representing a colony decrease of 26% after port closure.

Clutch interval

After port closure, average clutch interval was 37% longer than before, changing from 67 days (95% credible interval: 59–77) to 92 days (95% credible interval: 79–108).

Effect of food loss by port closure on breeding activity

Figure 1 shows reproduction parameters for the 4 years before and the 4 years after port closure. Table 1 shows the mean values for the years before and after port closure.

The number of breeding pairs per year fell significantly by 24.8% (95% Bayesian credible interval (BCI): –42.1%; –2.4%), and the number of nesting attempts per pair fell significantly by 28.5% (BCI: –38.0%; –17.4%) after port closure. However, mean clutch size did not change significantly. Overall, the number of eggs laid per year fell significantly after port closure by 45.6% (BCI: –63.1%; –20.0%).

There was no significant change in hatching success after port closure (4.5%; BCI: –22.3%;

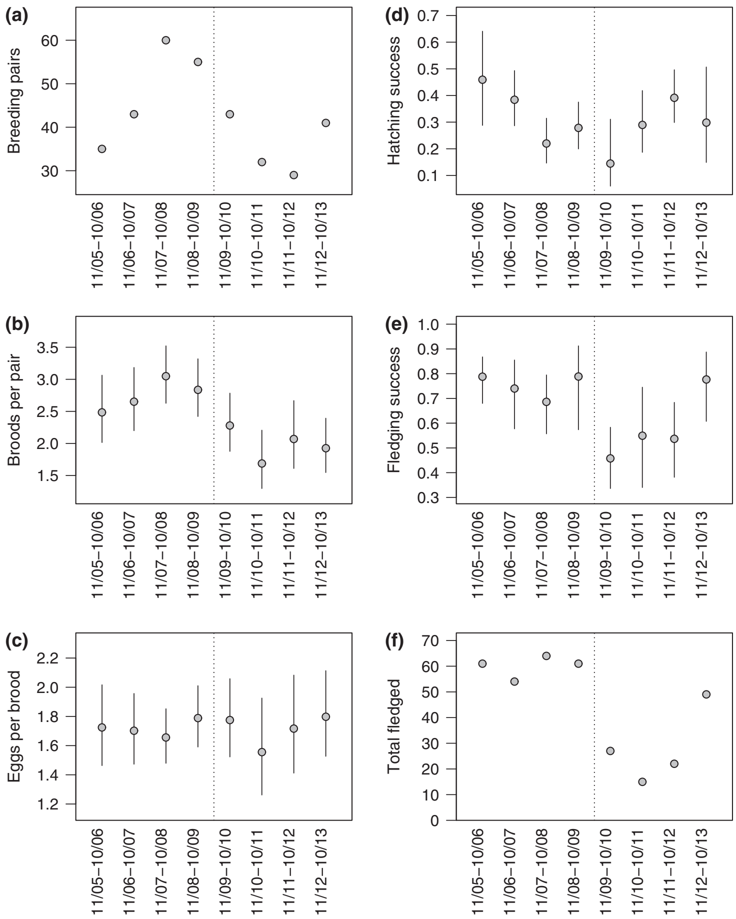

Figure 1. Subdivided annual reproduction parameters, indicated as November to October of the following year, of the Feral Pigeon population studied before and after a reduction in food loss. The vertical dashed line represents the closing of the Rhine Port St Johann, which is associated with significant food loss. Uncertainty is indicated by the vertical bar (95% Bayesian credible interval; exact values and their calculations are given in Table S1). (a) Breeding pairs, (b) broods per pair, (c) eggs per brood, (d) hatching success, (e) fledging success and (f) total fledged.

+40.8%), but fledging success decreased by 19.2% (BCI: –34.3%; –3.4%). The number of fledged young per pair per year (ARS), representing the accumulated impact of the port closure on the reproduction cycle up to the point of fledging, showed a marked reduction of 43.9% (BCI: –59.0%; –22.7%). Reduced fledging success of hatchlings combined with a reduced number of broods per pair after port closure are the main drivers of reduced overall reproductive success. In total, all of these effects combined to a significant reduction in the number of fledged young at the colony level of 54.6% (BCI: –68.9%; –33.2%) after port closure. The summarized numbers of breeding pairs, eggs laid, nestlings and fledglings of 4 years before food shortage and 4 years under food loss are shown in Figure 2.

DISCUSSION

In our long-term study of 831 Feral Pigeon broods, we were able to show that food shortage following port closure affected reproductive success at several stages of the reproductive cycle, notably the number of breeding attempts made by pairs within a season and the survival rate of hatchlings to fledging.

Table 1. Mean values of breeding parameters before (n = 4 years) and after (n = 4 years) port closure, and the corresponding change (percentage change relative to the value before port closure; with 95% Bayesian credible intervals given in parentheses). Same model types as for Table S1 (see Supporting Information), but now including before vs. after port closure as a fixed factor: year and breeding pair were random factors where values are not sums per year.

	Measurement level	Before port closure	After port closure	% difference
Breeding pairs	Year (n = 8)	47.9 (40.2; 57.4)	36.1 (29.7; 43.8)	–24.8% (–42.1%; –2.4%)
Nesting attempts	Year (n = 8)	130 (101; 167)	71 (54; 93)	–45.5% (–62.2%; –21.5%)
Eggs	Year (n = 8)	223 (171; 293)	121 (92; 160)	–45.6% (–63.1%; –20.0%)
Nestlings	Year (n = 8)	84 (68; 105)	47 (38; 60)	–43.9% (–59.0%; –22.7%)
Fledglings	Year (n = 8)	60 (46; 77)	27 (20; 36)	–54.6% (–68.9%; –33.2%)
Nesting attempts per breeding pair	Breeding pair (n = 338)	2.74 (2.50; 3.00)	1.96 (1.73; 2.21)	–28.5% (–38.0%; –17.4%)
Clutch size	Nesting attempt (n = 831)	1.71 (1.61; 1.83)	1.73 (1.58; 1.89)	+0.8% (–9.6%; +12.4%)
Hatching success	Nesting attempt (n = 831)	31.8% (24.7%; 39.7%)	33.2% (25.3%; 42.2%)	+4.5% (–22.3%; +40.8%)
Fledging success	Hatched brood (n = 328)	72.4% (63.8%; 79.7%)	58.5% (47.4%; 68.9%)	–19.2% (–34.3%; –3.4%)
ARS (fledglings per breeding pair per year	Breeding pair (n = 338)	0.83 (0.62; 1.13)	0.49 (0.35; 0.69)	–41.7% (–60.1%; –15.2%)

As the energetic costs for reproduction are higher for female than for male Feral Pigeons (Walsberg 1983), extra pressure is placed on females to find food. Pigeons in general have a long, sometimes even year-round, breeding season during which they lay multiple small clutches of almost exclusively two small eggs (Goodwin 1983, Robertson 1988). Once the eggs are laid, the energy expenditure of the incubation effort is minor. For both male and female pigeons, body weight increases during incubation accompanied by reduced food consumption, as the birds become relatively inactive while breeding (Riddle & Braucher 1934, Brisbin 1969). Clutches with only one egg, however, have a lower fledging rate than two-egg clutches (Johnston & Janiga 1995). This is because a singleton nestling may profit from more crop milk and food from both parents, but it suffers from the lack of reciprocal warming of another nestling. In Basel, the fledging success of one-egg clutches was about 10 times lower than that of two-egg clutches (Haag 1984).

The costs of reproduction are therefore relatively low up to the moment when the nestlings hatch. The number of young is thus limited by the energy needed to feed the nestlings. Energy requirements of two freshly hatched squabs with extremely high growth rates are difficult to meet, which consequently leads to a high mortality rate of the young, especially under food shortage conditions. In this study, the reduction in food caused by port closure resulted in a significantly larger number of the breeding pairs ceasing breeding. Pairs that continued to lay eggs produced significantly fewer clutches per year, with a significantly longer average clutch interval. Clutch size remained largely stable, possibly due to the low energy input required from both parents, and hatching success was unaffected. Fledging success was reduced after port closure, possibly because the feeding of the young is the most energy-demanding part of the reproductive cycle for the food-stressed adults.

Overall, food shortage reduced the total number of fledged young by more than half, which consequently led to a smaller colony size. However, except for the number of broods per pair, all results showed an apparent increase of the studied reproduction parameters in the 4th year after port closure (Fig. 1). It is conceivable that the Pigeons initially suffered from the sudden food loss, but eventually managed to compensate over time by finding food elsewhere. Additionally, the declining colony size might also have positively influenced the studied reproductive parameters through density-dependent processes.

Our findings show that when adults invest in a brood after port closure, the more limited food resource conditions mainly affected the nestlings. While the investments in egg synthesis and incubation are minor, the energy demands of raising a brood with two nestlings are high (Riddle & Braucher 1934, Brisbin 1969, Walsberg 1983). Food scarcity seems to be surmountable during the first part of the reproductive cycle, but it intervenes strongly at hatching. A reduction in clutch size from two eggs to one egg, which would increase the amount of food available per squab, is not effective because a single hatchling is not able alone to meet its thermoregulation needs.

Figure 2. Illustration of the summarized number of breeding pairs, eggs laid, nestlings and fledglings in 4 years under normal food conditions (left, green columns) and 4 years under food loss (right, red columns). The ratio of the number of nestlings hatched to eggs laid is given as hatching success; the fledging success depicts the ratio of fledglings to nestlings (average values from a binomial mixed model with breeding pair and year as random effects and before vs. after port closure as fixed effects).

Our prediction that Feral Pigeon pairs would lay fewer clutches in a season under food shortage was confirmed. Our prediction that hatching success would decrease because pigeons have to spend more time on foraging was not confirmed. This observation can possibly be explained because the needs of the newly hatched young can be met easily by small amounts of crop milk, even when food availability is limited. However, the significantly reduced fledging success is the crucial factor in the reproductive cycle, strongly limiting the reproduction of Feral Pigeons under food limitation.

In conclusion, the energy demands of older nestlings may cause mortality during the rearing phase when food scarcity limits the energy intake of the foraging parental birds. Thus, the ability of a nestling to fledge depends on the amount of food available to the parent birds.

These results are relevant in terms of the management of Feral Pigeon populations in urban areas. Applying the results in practice suggests that food limitations mostly affect the young birds, as more nestlings died after port closure. Feral Pigeon populations depend on abundant food for their maintenance and growth (Haag 1984). In urban areas, the available food base should not be supplemented by humans either intentionally or as human food waste. A more natural and ecological foraging behaviour would permit a healthier existence of Feral Pigeon populations in our cities, both for Pigeons and for people.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Reproduction data and respective food situation per year. The first five data rows contain simple yearly sums. The other values are mostly estimates from Poisson models, for Nl/Eg and Fl/Nl we used binomial models (number of successes vs. number of failures); in all cases, only an intercept was estimated. An observation-level random factor was included when overdispersion was indicated (residual deviance much larger than residual degrees of freedom, or using the function disperson_glmer from the R-package blmeco for mixed models). Where the value is per brood (Eg/BR, Nl/BR, Fl/BR), the breeding pair was included as a random term. Bayesian 95% credible intervals are given in parentheses. Abbreviations: normal = normal food situation, food loss = loss of main food source due to closing of the Rhine Port, BP = estimated number of breeding pairs, BR = broods, Eg = eggs, Nl = nestlings, Fl = fledglings, ARS (annual reproductive success) = fledglings per breeding pair. Standard deviations are given in parentheses.

Chapter 5

Host finding of the pigeon tick *Argas reflexus*

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Host finding of the pigeon tick *Argas reflexus*

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Abstract. The medically and veterinary important feral pigeon tick *Argas reflexus* (Ixodida: Argasidae) Fabricius usually feeds on pigeons, but if its natural hosts are not available, it also enters dwellings to bite humans that can possibly react with severe allergic reactions. *Argas reflexus* is ecologically extremely successful as a result of some outstanding morphological, physiological, and ethological features. Yet, it is still unknown how the pigeon tick finds its hosts. Here, different host stimuli such as living nestlings as well as begging calls, body heat, smell, host breath and tick faeces, were tested under controlled laboratory conditions. Of all stimuli tested, only heat played a role in host-finding. The heat stimulus was then tested under natural conditions within a pigeon loft. The results showed that *A. reflexus* is able to find a host over short distances of only a few centimetres. Furthermore, it finds its host by random movements and recognizes a host only right before direct contact is made. The findings are useful for the control of *A. reflexus* in infested apartments, both to diagnose an infestation and to perform a success monitoring after disinfestation.

Key words. *Columba livia*, body heat, ectoparasite, feral pigeon, host cues, host detection, host stimuli.

Introduction

The pigeon tick *Argas reflexus* Fabricius belongs to the veterinary and medically important tick species. The hematophagous ectoparasite inhabits the nesting and roosting sites of feral pigeons *Columba livia* (Columbiformes: Columbidae) Gmelin. It naturally feeds on feral pigeons but uses humans as substitute hosts when pigeon density is low or when pigeons are completely absent. *Argas reflexus* is not able to establish a population solely on human blood as the ticks die after they have fed on humans (Kemper and Reichmuth, 1941). Therefore, human *A. reflexus* infestation can always be traced back to an animal host, almost exclusively feral pigeons.

In human buildings in central Europe, *A. reflexus* is predominantly an urban pest (Dautel *et al.*, 1999). It is mainly nocturnally active and spends most of its life off-host, hidden in cracks and crevices. Its thigmotactic behaviour forces the pigeon tick to bring as much of its surface as possible in contact with external structures.

Each developmental stage of the very host-specific *A. reflexus* feeds in the urban environment exclusively on feral pigeons, and as an Argasid typically remains within the nest or burrow of its hosts (Klowden, 2010). *Argas reflexus* accordingly hides in the direct surroundings of pigeon nests. In general, the nest environment provides ideal conditions for nidiculous tick development off the host, reproduction, sustenance for the various feeding stages and a high probability of host presence (Anderson and Magnarelli, 2008).

The larvae usually hatch during the summer months when the climatic circumstances guarantee good development for the ticks themselves and more importantly for the young feral pigeons. The numerous pigeon nestlings in the close vicinity offer a convenient food basis for all blood-sucking stages of *A. reflexus*. This is important especially for the larvae that need their first bloodmeal within a short period of time after hatching.

The main reasons for the ecological success of *A. reflexus* are its long life expectancy of 7–11 years or even longer (Dautel and Knülle, 1997a) and some outstanding morphological, physiological and ethological features that help it save energy between the bloodmeals and enable the nymphal and adult ticks to survive for up to 9 years without food (Kahl, 1989; Dautel and Knülle, 1996, 1997b; Dautel *et al.*, 1999; Dautel, 2001).

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Argas reflexus usually only searches for a substitute host when its natural pigeon host is not sufficiently available or lacks completely. As a result of the specific condition of the synanthropic environment, humans are the most common substitute hosts because wandering ticks penetrate into the human lodging (Karbowiak and Supergan, 2007). Pigeon tick bites may produce allergic reactions of diverse severity presumably caused by the proteins secreted by the tick's salivary glands (Sirianni *et al.*, 2000). Dramatic symptoms of an anaphylactic shock including shortness of breath and loss of consciousness occasionally may occur (Haag-Wackernagel, 2005; Kleine-Tebbe *et al.*, 2006). Hilger *et al.* (2005) were able to identify and characterize Arg r 1 as the major allergen responsible for anaphylactic reactions caused by bites of the pigeon tick *A. reflexus*. Fatal cases are rarely reported owing to the difficulty in tracing back to *A. reflexus* as the parasite quickly disappears after a bite. However, Buczek & Solarz (1993) reported a case of a 42-year-old-man that died of an anaphylactic shock after four *A. reflexus* attacks.

Until today, it is unknown how this tick species finds its host. Howell (1975) speculated that for ticks that inhabit the roosting or nesting substrate of their hosts, as e.g. the pigeon tick, ambulations, which result in host encounter, apparently occur without direct stimulation from the host. Schulze & Schröder (1949) discovered that *A. reflexus* appears to have a low distance perception of host proximity. In their study, it seemed that *A. reflexus* recognizes or discriminates its host only centimetres away, right before actual contact.

The present study was conducted to characterize the responsiveness of *A. reflexus* to different host stimuli under controlled laboratory conditions. During the second part of this study, a then determined attractive stimulus was tested under natural conditions within a pigeon loft.

Materials and methods

General experimental laboratory setup

The laboratory experiments were performed between September and December 2014. Female pigeon ticks were collected out of cracks and crevices in the pigeon loft of the Matthew church in Basel (47°34′2″N, 7°35′35″E), Switzerland. The females were then individually stored in test tubes sealed with a fine net. A $2 \times 4\,cm^2$ filter paper strip was placed in the test tubes onto and under which the ticks could crawl, defecate and lay their eggs. Out of all the *A. reflexus* larvae that hatched from eggs laid in the laboratory, 176 were used in the laboratory experiments.

All test tubes were kept in a desiccator at room temperature in darkness. Inside the desiccator, a RH of 75% was obtained with the help of a saturated sodium chloride solution. To guarantee that the larvae were hungry and willing to search for a potential host, the freshly hatched larvae were kept for a minimum of 25 days individually stored in test tubes in the desiccator before they were used in the host stimuli trials. The test tubes containing the larvae were taken out of the desiccator at least 30 min before each trial and kept in complete darkness until right before the trial started.

The experimental setup, here defined as an arena, consisted of a circle with a diameter of 15 cm being printed on a piece of paper. Degree values (from 0 to 360°) were written around the arena and the tested stimulus was placed 1.5 cm outside of the arena at the 90° mark. For each trial, a single larva was placed in the middle of the arena by gently letting it slip out of the tube. After the test tube was removed, the larva was allowed to locate the stimulus. In total, the distance between stimulus and the larva's starting point in the middle of the arena was thus 9 cm. For each trial, the degree value at which the tick left the circle was recorded. If the larva did not leave the circle within 20 min, the trial was stopped. To avoid bias originating from the present additional host, a glass plate was set up between the ticks and the experimenter. The stimulus direction was randomly chosen to be either on the left or right side of the experimental setup. With the stimulus placed at 90°, values below 180° symbolized thus a locomotion towards the stimulus, whereas values above 180° displayed movements away from it. The experiments were performed at room temperature and steady laboratory conditions with an overhead dim light (< 5 lux). The light intensity was defined with a lux meter (HoldPeak, Ebern, Germany) before each trial. Ventilation was turned off during the experiments so that no air currents could influence the trials. For each category, a number of 40 larvae were tested individually.

After five trials, the table on which the experimental sheet was placed, was cleaned with 70% ethanol, dried and a new experimental sheet was used. After the trial, each larva was allowed to rest in complete darkness in a test tube in the desiccator for a minimum of 24 h. Immobile specimens were tested for viability by irradiating them with an intensive light pulse. Only physically fit larvae were used. The following host-related stimuli were tested in the laboratory:

1. *Nestling – control*: Two 23- to 24–days-old nestlings from the experimental pigeon loft were brought into the laboratory to create a situation similar to natural conditions. To keep the nestlings in place, they were set into a circle of wire mesh with a 27 cm diameter. The bottom of the wire mesh barrier was lined with clean gauze and paper towel. The nestlings were set side by side in the circle, according to their preferred natural sitting position. The wire mesh barrier, behind which the nestlings served as a natural stimulus, was thus placed at the 90° mark.
   As control stimulus, the gauze and the paper towels were removed. The barrier was cleaned with 70% ethanol and used without the nestlings.
2. *Begging call – no sound*: The recorded begging calls of two nestlings were played from a loudspeaker (model PX-3619-675 from auvisio; PEARL Agency GmbH, Buggingen, Germany). These calls are typically produced to attract the attention of the parental birds when the hungry nestlings want to be fed. The loudspeaker was placed vertically at the 90° mark. The noise was thus directed into the middle of the arena where the larvae were placed.
   As a control for the begging call trials, the loudspeaker was turned on and positioned similar to the begging call trials but no sounds were emitted.
3. *Body heat – room temperature*: To test whether *A. reflexus* larvae are attracted to body temperature, a heat source with the same size as the two nestlings previously used was built. The heat source consisted of a rolled up flexible tube

through which tap water heated up to 37–38 °C circulated. Before each trial, the surface temperature of the tube was controlled with an infrared thermometer (Medisana, Neuss, Germany). Additionally, the surface temperatures of the arena were measured at 1.5, 9 and 16.5 cm away from the heat source.

As a control, the same setting was used but the tap water circulated through the tube at room temperature.

4 *Smell – no smell*: Fifty grams of the gauze and the paper towel that were used as a bottom for the nestling barrier in the first trial were used as the smell from hosts. The gauze and the paper towel were placed without any barrier at the 90° mark.

As a control, sterile gauze and clean paper towel of the same quality and quantity were used.

5 *CO_2 – air*: The gas mix used for this study, hereinafter called 'CO_2' for simplicity, imitated the hosts' exhaled air and consisted of a mix of 78% nitrogen, 18% oxygen, 3% carbon dioxide and 1% inert gas in the same proportion as air (calculated after Butler *et al.*, 1977). The gas mix was delivered in a 10-L aluminium bottle containing 150 bar (Carbagas, Guemligen, Switzerland).

The control stimulus was room air drawn in by a pump (Analyt-MTC GmbH, Müllheim, Deutschland). The CO_2 and the ambient air were pumped through a 6-mm-diameter tube with an intercalated flow meter (Kytola, Muurame, Finland) constantly measuring the flow rates. The end of the tube was fixed at the bottom of the arena at the 90° mark, thus directly letting the gases flow into the middle of the arena were the larvae started. Based on the study of Calder & Schmidt-Nielsen (1966), the flow rates of both CO_2 and ambient air were set at 400 mL/min, thus referring to the volume exhaled by two pigeons.

6 *Faeces – no faeces*: The filter paper strips onto which the ticks defecated when being stored in the test tubes in the desiccator were used as the source of a possible natural assembly pheromone. The $2 \times 4\,cm^2$ paper strips were placed flat on the bottom next to the arena at the 90° mark.Clean, unused filter paper strips of the same size served as controls.

Experimental setup in the pigeon loft

The experiments in the pigeon loft were performed between March and April 2015. Four analogue-heated pigeon models, here defined as artificial pigeons, were built and consisted of a plastic jar with a volume of 1 L. In the middle of the jar, a heating cable (Zoo Med Laboratories Inc., San Luis Obispo, CA, U.S.A.) was inserted and the remaining cavity was filled with sand as isolating material. These artificial pigeons were then placed on a sheet of experimental paper within a $21.5 \times 12\,cm^2$ area covered with double-sided adhesive tape onto which the ticks would get stuck when trying to reach the artificial host. Two different sampling places were chosen, one with numerous active nests in close distance (site 'near' henceforth), and one at the opposite site of the pigeon loft with only one breeding place (site 'far'). For each place, two artificial pigeons were set up, one was randomly chosen to be heated while the other was placed 1 m away and served as a control.

The surface temperature of the heated artificial pigeon ranged from 37 to 42 °C. The unheated control artificial pigeon had an ambient temperature. To keep the same temperature range for each trial, a thermoregulator (Tinxi.com GmbH, Eggenstein-Leopoldshafen, Germany) was interconnected. Each trial lasted for 7 days. At the end of each trial, the experimental papers of the heated models and the controls were collected and the stuck hungry tick larvae were counted under a binocular microscope. During this visual examination, it was confirmed that the larvae were flat, had a light body colouring and had thus never consumed a blood-meal before. Therefore, they were defined as hungry.

Statistical analysis

Experiments in the laboratory were analysed separately for each type of stimulus. If the tick did not leave the circle within 20 min, the case was discarded. There were 0–2 such cases, except for the stimuli room temperature and CO_2 with 5 cases each, and the stimulus no faeces with 7 cases.

Several statistical tests were performed for the direction of movement. The Rayleigh test was used to test whether the directions were clustered in one direction. Because this test would not indicate a multi-modal deviation from a uniform distribution of the directions (e.g. a clustering in two directions), the Watson goodness-of-fit test, a non-parametric test that compares the observed distribution with a uniform distribution, was also used. To compare the directions between a stimulus and its control, the Mardia–Watson–Wheeler test was used.

Data from the experiment with the artificial pigeons in the loft were analysed using a separate Poisson linear mixed model with log-link for the two locations within the pigeon loft ('near' and 'far', see above). The Poisson model is the most suitable model for count data. The count data here were the number of ticks found on the adhesive tape. The date (number of days since the start of the experiment) was used as a covariate, 'treatment' (with the levels 'heated' vs. 'control') as a fixed factor. 'Pair' (the treatment and control sample performed concomitantly) was included as a random factor to account for the paired design of the experiment. No strong overdispersion was observed and graphical residual analyses showed satisfactory performance of the model. To draw inferences, 10 000 values were sampled from the posterior distribution assuming flat priors using the R-function sim from the package arm. The model estimates are given with the 95% Bayesian credible intervals (i.e. the true value is expected to be within this interval with a probability of 95%).

Statistical analyses were conducted using the open source software R (R Core Team, 2014; Version R3.0.3 for Mac), and its packages 'circular' (Version 0.4-7) and 'arm' (Version 1.7-07).

Results

Experiments in the laboratory

The directions at which the larvae left the arena were traced for each trial. By testing the observed directional movements of the larvae for significance, three different statistical tests were used (Table 1). For each stimulus, the tests are independently discussed below.

1 *Nestling – control*: The directions and distributions of the larvae differed neither from a uniform distribution around the circle (Rayleigh test and Watson test) nor between the two stimuli nestling and control (Mardia–Watson–Wheeler test).
2 *Begging call – no sound*: The statistical tests did not indicate a significant deviation of either of the two distributions from a uniform distribution around the circle (Rayleigh and Watson tests) nor a difference of the directional distributions of the larvae in the begging call vs. no sound trials (Mardia–Watson–Wheeler test).
3 *Body heat – room temperature*: The larvae preferred the direction towards the body heat stimulus (Rayleigh test, $Z = 0.557$, $P < 0.001$). This was not the case for the room temperature stimulus (there was a trend for a preferred movement in the opposite direction of the stimulus, but with a lot of scatter, $Z = 0.28$, $P = 0.06$). There was clear evidence of a difference in the observed directions between the body heat stimulus and its control (Mardia–Watson–Wheeler test, $W_g = 22.8$, $P < 0.001$).
4 *Smell – no smell*: The tests showed a significant concentration roughly towards the no smell stimulus (Rayleigh test, $Z = 0.28$, $P = 0.045$). However, the distributions of the two stimuli smell and no smell did not differ significantly according to the Mardia–Watson–Wheeler test ($W_g = 2.55$, $P = 0.10$).
5 *CO_2 – air*: The Watson test indicated a tendency of a non-uniform distribution around the circle for the CO_2 stimulus ($U^2 = 0.16$, $0.05 < P < 0.1$). The average direction was oriented towards 92°, right where the stimulus was placed. However, the Rayleigh test did not indicate a strong directional clustering of the points ($Z = 0.20$, $P = 0.23$), nor was there an indication of a different directional distribution between CO_2 and its control, air.
6 *Faeces – no faeces*: For the faeces stimulus, the Watson test indicated a deviation from a uniform distribution around the circle ($U^2 = 0.19$, $0.025 < P < 0.05$), with a possible clustering towards the stimulus, although this signal was rather weak (Rayleigh test, $Z = 0.25$, $P = 0.09$). Also, there was no indication of a strong difference from the control treatment.

Experiments in the pigeon loft

The hungry larvae were significantly more attracted to the heated model compared with the control model at both sites. While the average number of ticks found on sticky paper at site 'near' and during the beginning of the experiment (on day 8, i.e. when the ambient temperature was still lower, see discussion) was 54 (with a 95% Bayesian credible interval of 35–82) for the heated artificial pigeon, the control generated only an average of 12 individuals (7; 19). Fewer ticks were caught at site 'far' but again the heated artificial pigeon attracted 11 ticks (5; 28), whereas the control attracted only 4 (1; 10). Additionally, declining tick numbers and a declining absolute difference between the two pigeon models over time were observed (Fig. 1A, B). The effect of time was significant for both models: −0.020 (−0.039; −0.002) ticks on the log-scale per day for site 'near', −0.045 (−0.084; −0.006) for site 'far'.

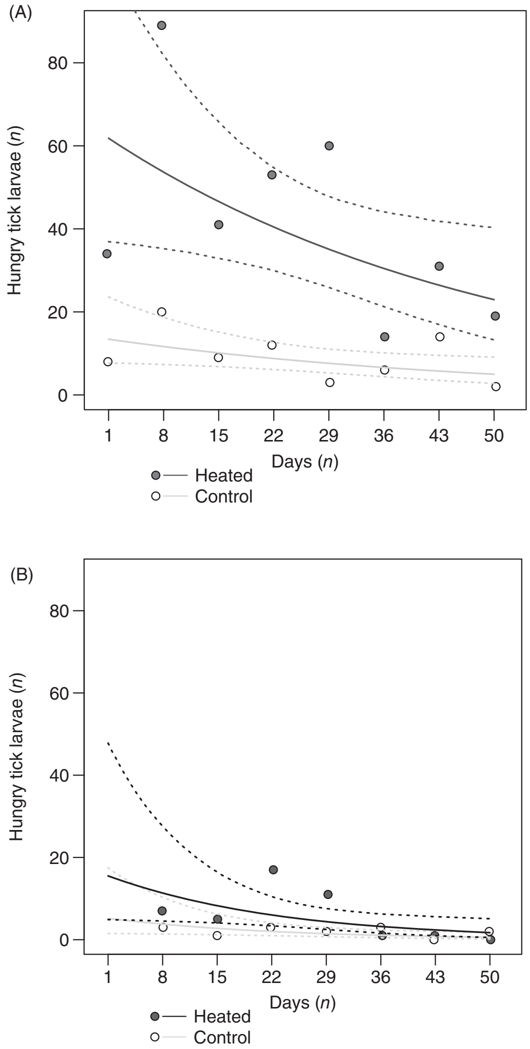

Fig. 1. Number of flat, lightly body coloured and thus hungry tick larvae collected over time. Number of hungry tick larvae collected on sticky paper around a heated (dark grey) or control (light grey) artificial pigeon over time (day 1 = 11. March, then 7-day intervals between trials) separately for a site near several pigeon nests (A), and farther away from most pigeon nests (B). Raw data (circles) and model predictions (lines with Bayesian 95% credible interval as dashed lines; Poisson mixed model, compare Table S1 in the supporting information section for parameter estimates) are given.

Table 1. Tested host cues statistically analysed for a potential defined movement of larvae.

	Rayleigh test		Watson test		Mardia–Watson–Wheeler test		
Stimulus	Z	*P*	U^2	*P*	W_g	d.f.	*P*
Nestling	0.157	0.385	0.083	> 0.1	0.524	2	0.769
Control	0.078	0.79	0.059	> 0.1			
Begging call	0.202	0.213	0.111	> 0.1	1.508	2	0.471
No sound	0.023	0.98	0.024	> 0.1			
Body heat	0.557	< 0.001	0.691	< 0.01	22.838	2	<0.001
Room temp	0.279	0.064	0.155	$0.05 < P < 0.1$			
Smell	0.236	0.107	0.14	> 0.1	4.55	2	0.103
No smell	0.277	0.045	0.195	$0.025 < P < 0.05$			
CO_2	0.204	0.234	0.158	$0.05 < P < 0.1$	3.302	2	0.192
Air	0.112	0.622	0.051	> 0.1			
Faeces	0.254	0.085	0.192	$0.025 < P < 0.05$	1.71	2	0.425
No faeces	0.096	0.743	0.039	> 0.1			

Discussion

The feral pigeon is a worldwide distributed, very successful commensal urban bird species that lives very close to the human population. Wild urban pigeons commonly roost and nest in living quarters. As a result of their proximity to humans, the risk of humans being infected with zoonotic diseases and parasites originating from the birds increases. Feral pigeons can transmit multiple parasites, but the pigeon tick *A. reflexus* is the most important health risk from feral pigeons (Haag-Wackernagel, 2005). Its bites may have substantial impacts on health. Repeated bites may even lead to an anaphylactic shock with a potentially fatal outcome (Buczek and Solarz, 1993).

Larvae of the pigeon tick have the shortest survival time without a bloodmeal. Hence, they depend on an efficient host-finding mechanism. In this study, the host finding behaviour of *A. reflexus* larvae was examined. It was hypothesized that *A. reflexus* larvae perceive stimuli only at very close ranges of just a few centimetres. During the laboratory experiments larvae, that had never eaten a bloodmeal before and were thus hungry, were exposed to potentially important stimuli. Living nestlings, begging calls, body heat, smell, host breath and tick faeces were tested individually as larvae stimuli in comparison to control stimuli. The experiments showed that heat was the main stimulus that guides *A. reflexus* to its host. The other tested stimuli did not result in a comparable strong force of attraction.

Surprisingly, a heat source attracted more larvae than the real living host. The nestlings moved within the wire mesh and thus sometimes increased the distance to the larvae while the tube that was used as the heat source remained motionless in place for the entire experimental trial. It seems as if those few centimetres must make the decisive difference of the larvae finding the stimulus.

Heat is known to be a common stimulus for hematophagous parasites. The chicken mite *Dermanyssus gallinae* (Mesostigmata: Dermanyssidae) (De Geer), for example, is clearly sensitive to temperature changes as a cue to detect a potential host (Kilpinen and Mullens, 2004). Webb (1976) discovered that the tick *Ornithodoros concanensis* (Acari: Argasidae, Cooley and Kohls, 1941) did not react with carbon dioxide, but was attracted to a heat source. However, it appears unimportant in long-distance host detection and is perceived only at very close range Webb (1976). Furthermore, the tick *Argas cooleyi* (Acari: Argasidae, Kohls and Hoogstrahl, 1960) finds its host by apparently undirected orientation, but host cues such as body heat, host odour and breath are attractive at a short range (Howell, 1975). When looking at the distance that a heated object radiates heat, it becomes clear why heat functions as a short distance host stimuli only. The radiant heat of an object that is slightly warmer than its surroundings cools down at very short distances. During the laboratory experiments, the surface temperature dropped by 13 °C within a distance of only 1.5 cm. In the middle of the arena, 9 cm away from the heat source, the temperature was only 0.05 °C above room temperature. Furthermore, Webb (1976) used a vial heated up to 40 °C as an artificial host for his study on *O. concanensis*. The study shows that the temperature dropped from an artificial host of 40 °C down to 31 °C at only 1 cm distance (30 °C at 2 cm; 29 °C at 3 cm). Consequently, a parasite that is attracted by heat finds its warm-blooded hosts only at very short distances of a few centimetres.

While testing the heat stimulus within the pigeon loft, the hungry larvae were significantly attracted by the heat source. Also, tick numbers and the absolute difference between the two pigeon models (heated and control) declined over time. This is in conjunction with findings of Dethier (1957) who states that the absolute temperature of a warm object, provided it lies below 40 °C, is of no significance. Important is the difference between this temperature and that of the surroundings. In the course of the experiments in the pigeon loft, the temperature increased over the experimental time (ambient temperature in March: 8–10°; in April 14–19°). The thermal differences between the heated artificial pigeon and the control at an ambient temperature also decreased and thus might have been less obvious to the hungry *A. reflexus*. It is also possible that fewer ticks got caught over time at the adhesive tape because the larvae that got stuck on the tape were removed from the current population and thus fewer ticks were available in April than in March.

The begging calls had no effect on *A. reflexus* larvae, which was in contrary to findings of Webb *et al.* (1977) who discovered that the begging sound was used as a host-detection cue for the soft tick *O. concanensis*, a parasite of cliff swallows *Petrochelidon pyrrhonota* (Passeriformes: Hirundinidae) Vieillot.

A statistically significant difference between the smell and the no smell stimulus was not found. In general, the host smell is thought to be an important stimulus for other hematophagous parasites. However, it makes sense that *A. reflexus* is not attracted by the smell of feral pigeons because of the close range of the hosts habitat. Feral pigeons typically live in crowded smelly breeding places where a smell gradient is absent. This is also highlighted by the fact that to parasitize a host, hematophagous arthropods must first identify and locate the host amid all other stimuli that are present: a considerable challenge in a complex environment replete with signals (Klowden, 2010). This is probably especially difficult for nest-dwelling ticks as e.g. *A. reflexus*. Although the host smell was not identified as a stimulus attracting *A. reflexus* in this study, it might be interesting to test in the future how the ticks react towards exhaled air from feral pigeons as this transports host odour in high concentrations.

In the CO_2 trial, neither was the directional clustering strong nor was there a statistically significant different distribution between CO_2 and the air stimulus. This observation confirms another study in which 5% CO_2 failed to evoke positive responses in unfed nymphal *Ornithodoros concanensis*, the ticks of cliff swallows Webb (1976). Thus, CO_2 is not an important stimulus to nidiculous ticks. For other tick species, that must sense their hosts over greater distances this stimulus might be of importance.

The results showed a weak clustering towards the pigeon tick faeces stimulus. This behaviour was expected to be more pronounced as Sonenshine (2006) states that when ticks come in contact with other conspecific individuals, or with waste material deposited by such individuals, they cease activity and remain quiescent. Furthermore, the constituents of tick faeces and exuvia comprise the active components of arrestment or assembly pheromones, which are particularly widespread in nidicolous soft ticks (Allan, 2010). These pheromones cause locomotion to stop and result in clusters of individuals in the environment which may enhance contact with potential hosts, enhance survival by keeping ticks in favourable microhabitats and ensuring mating for those species that mate off hosts (Allan, 2010). Successful feeding on a host, signalized by the following excretion of waste material, thus might help nidicolous *A. reflexus* to stay not only within the proximity of its host but also to rest within physiologically ideal microhabitats that enhance the chance of mating. As the here tested larvae have no need to find other *A. reflexus* ticks, tick faeces might be more attractive to adult stages that have to establish a population and are, therefore, in bigger need of finding other conspecifics.

In conclusion, the main stimulus that guides *A. reflexus* to its hosts is heat. Movements of the pigeon tick within its habitat seem to be initially random until a specific heat stimulus is encountered. The heat stimulus functions only over short distances, within the very close range of a pigeon nest. Given the living condition of *A. reflexus* this behaviour makes perfect sense as it spends its entire life close to its host.

The results are useful for the control of *A. reflexus* in infested apartments, both to diagnose an infestation and to perform a success monitoring after disinfestation.

The ecological success of the pigeon tick is as a result of its extraordinary physiological features, as e.g. long life expectancy, long-term starvation capability and tolerance of temperature extremes. Eradication of pigeon colonies or installation of deterring systems that exclude the birds from their roosting places in urban living areas leads to deprivation of the parasites' food source. This, in turn, forces *A. reflexus* to wander out of its shelters, enter human living spaces and encounter humans. *Argas reflexus* infestation can always be traced back to feral pigeons, as the host-specific ectoparasite is not able to establish a population solely on human blood (Kemper and Reichmuth, 1941). Given the worldwide increasing feral pigeon population, the risk for *A. reflexus* infestations needs careful monitoring as an emerging parasite with a considerable pathogenic potential.

Therefore, it is strongly recommended that specialists (e.g. pest control companies) perform the following steps in the case of an *A. reflexus* infestation: search and identification of *A. reflexus*, questioning of neighbours, search for sting reactions and possibly found unidentified arthropods, in-depth quest for close-by pigeon roosts as an infestation source, elimination of the infestation source, cleaning and disinfestation of formal pigeon breeding sites, performance of pigeon exclusion measures and finally a control of success.

Animal welfare

The study conformed to Swiss law on animal welfare. The experiments were conducted with the animal experimental permission of the Cantonal Veterinary Office of Basel-Town, Switzerland (authorization No. 2596).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/mve.12165

Table S1. Parameter estimates for the Poisson model with log-link fitted to the number of ticks found on adhesive tape around a heated versus a non-heated control artificial pigeon. One model each was fitted for the data from the two sites 'near' (near several breeding boxes) and 'far' (farther away from most breeding places). The reference level for treatment was the control with ambient temperature. The interaction between treatment and date and a quadratic effect of date were not included in the models based on their credible intervals (which spanned across 0).

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Chapter 6

Discussion and General Conclusion

6 Discussion and General Conclusion

6.1 Discussion

The aim of this thesis was to contribute to a better understanding of feral pigeons. It focuses on different questions concerning the epidemiology, biology and food-dependent reproduction of the birds. As chapters 2–5 cover different topics, they are discussed separately. A general conclusion is given at the end of this chapter.

Chapter 2 shows the results of a study conducted in the experimental loft to evaluate the effectiveness of gel repellents on feral pigeons. While numerous avian proofing systems are regularly introduced onto the market, scientific proof of efficacy and their use from the point of view of animal welfare is lacking. Therefore, two gel repellents, one contact gel and one optical gel were tested. The study showed that both gels were not completely effective, meaning that a reduction in the number of birds using the protected structures by 100% was not observed.

The mechanism of the tested contact gel is supposedly based on a slight irritation of the birds by means of capsaicin, the pungent element of red pepper. While capsaicin is an extremely effective irritant for mammals, birds are almost totally insensitive to it (Szolcsányi *et al.*, 1986; Mason *et al.*, 1991; Clark, 1997; Mason, 1997; Mason, 1998). For this reason, a claimed sensory reaction to the gel, as stated by the distributor, was neither expected, nor was it observed during trials. Instead, startle responses due to neophobia and discomfort were thought to be responsible for the mild repellent effect. As a consequence, the pigeons seemed to get used to the substance over time. Additionally, the gel had an unpleasant esthetic aspect and a limited life span due to fouling with dust, insects, feathers and feces. Furthermore, the possibility of gluing of plumage as well as of affecting other structures and non-target birds is possible when using it under realistic and not experimental conditions. Due to these reasons, this tactile gel cannot be recommend in feral pigeon proofing.

The tested optical gel also failed to achieve complete effectiveness. According to the distributor, the product is able to repel birds visually because it is perceived as fire in their ultraviolet visual spectrum. Additional natural oils that should be abhorrent on an olfactory, gustatory and tactile basis reinforce the repellent effect according to the distributor. The reasoning for the birds seeing the optical gel as fire could not be confirmed in this study. Furthermore, observations of the feral pigeons reacting to the optical gel suggest that it does not work on the above-mentioned senses of pigeons.

Summarizing, both gels seemed to have only an ineffective, non-permanent repellent effect and displayed questionable characteristics in terms of animal protection. The gels were spread all over the experimental loft, so that even birds not flying onto the prepared structures came into contact with gel residues.

The study was presented at a pest control conference. In the course of the presentation, several pest controllers criticized the gels as they have had bad experiences with their use. In addition, they confirmed that a satisfying effectiveness of the gels was not observed in the course of their work. One of them was even asked to remove the optical gel from a rooftop as it had caused more damage by soiling the roof than actually repelling pigeons. In the course of the conference, the large majority of the pest controllers stated that they would welcome a scientifically implemented testing phase of new feral pigeon proofing systems before they are introduced onto the market.

This study shows how important it is to put new feral pigeon proofing systems to the test before their application. An evaluation on the part of a qualified testing agency would not only benefit the user who expects high efficiency, but more so it would protect the birds from unnecessary pain.

Chapter 3 offers an overview of the most essential pigeon proofing systems, such as bird nets, wire mesh, electroshock systems, sharp and blunt metal spikes, synthetic spikes, tension wire and gels. It describes each system and defines its advantages and disadvantages. Furthermore, the problem of unevaluated systems that lack proof of efficacy and a classification of their use in terms of animal protection is pointed out. This chapter also brings up further difficulties, such as the lack of maintenance of alleged harmless systems and their incorrect installation.

This chapter further illustrates that the free-living feral pigeon populations are exposed to the same natural selection as any other wild living species. From a biological point of view, they therefore have to be considered as wildlife that has adapted to the city habitat (Köhler, 2008). In Switzerland, feral pigeons are legally regarded as wildlife. In Germany, however, feral pigeons are, from a legal point of view, referred to as ownerless domestic animals and are not subject to the German hunting law. Instead, they belong to the vertebrates without particular protection status and are solely protected by the animal protection act. The German animal protection act states, among other things, that no person may, without good cause, inflict pain, suffering, injury or lasting harm on any animal. It further forbids the use of devices and substances in order to catch, repel or scare off vertebrates if this is linked to the risk of avoidable pain, suffering or injury of the vertebrates. Experiments with free-living feral pigeons demonstrated that highly motivated individuals are able to surmount almost every proofing system (Haag-Wackernagel, 2000). Another study showed that brutal pigeon proofing systems, which intentionally aim at hurting the birds, do not show better efficacy than harmless systems (Haag-Wackernagel, 2010b). Solely and exclusively the motivation of the pigeon determines whether the bird will try to surmount an installed proofing system or not. Systems that intentionally inflict pain, suffering, injury or lasting harm to feral pigeons are therefore not only legally forbidden, but they also lack scientific validation.

Feral pigeon proofing systems enjoy wide popularity because the soiling of house facades and other structures leads to inconveniences and high cleaning costs. In addition, homeowners fear problems with emigrating material pests as well as the transmission of pathogenic microorganisms and parasites. However, feral pigeons are adaptable and intelligent, which makes it difficult to repel them. They are able to use ledges and openings of only a few centimeters width (Haag-Wackernagel and Geigenfeind, 2008). Moreover, the birds are imprinted on their breeding places, which is why they persistently try to reach them. It is therefore much more difficult to repel feral pigeons from an already infested building, than to architecturally hinder the birds from roosting and breeding at new, unaffected house facades by avoiding pigeon-attractive structures during building design (Haag-Wackernagel and Geigenfeind, 2008).

The perfect feral pigeon proofing system has yet to be invented. It would have to be cheap, visually inconspicuous, efficient, long lasting and, most importantly, it would have to conform to animal welfare laws. Unfortunately, there are plenty of cases in which feral pigeons are either trapped, injured or even killed by falsely installed or poorly maintained proofing systems. Even systems that conform to animal welfare can become harmful if they are falsely mounted or badly and irregularly maintained. For example, bird nets that lack any tension at installation do not efficiently proof a structure. Also they are not safe for the birds because they can become entangled in the loose mesh. Even worse is the fact that, in most of these cases, the simple lack of awareness of the end users leads to these unintentional incidents. In summary, only tested, as well as correctly installed and maintained systems can meet the requirements of animal welfare. A proper application and maintenance guide published by manufacturers and certified by animal welfare authorities could prevent the animals from being harmed. Additionally, this would provide legal protection to end users who are not familiar with bird proofing systems.

The chapter points out the inconsistency of what the law demands and what is actually being carried out in practice. It supports the idea of an easy to understand application and maintenance guide that should be delivered with each system. Ideally, a test seal could label systems that conform to animal protection. Until then, the only general basis on which an objective evaluation of each system is possible is a scientific study that puts the systems to the test. Ironically, each scientifically performed study that uses animals needs the approval of the animal testing authority and has to be performed under strict conditions. In case the experiment cannot be performed within these limits, it has to be stopped. However, feral pigeon proofing systems are regularly introduced onto the market without being tested with regard to animal welfare. Instead, they are being put to the test in practice.

Chapter 4 deals with the effect of a breakdown in the food basis on the reproduction of a well-studied feral pigeon breeding colony. This study was performed under natural living conditions. It covers breeding data from eight consecutive years, of which four were during the food shortage. Besides diseases, parasites, stress and a limited number of breeding places, the biggest of all environmental challenges that feral pigeons have to face is finding sufficient food. While most birds depend on naturally accessible food sources, synanthropic birds, such as feral pigeons, have their own particularities when it comes to fluctuations in food supply. They strongly depend on intentional feeding by humans and their food waste in urban surroundings. However, feral pigeons are also able to quickly react to environmental changes due to certain physiological features regarding their reproduction. If feeding conditions are ideal, they are able to achieve a great number of broods leading to a large number of fledged young.

Despite the well-known fact that food shortage is a major source of reproductive failure in feral pigeons, it was still unclear at which phase of the reproductive cycle it reduces overall reproductive success. The colony that was studied to clarify this important question foraged mainly at the nearby Rhine Port, where tons of grains were spilled, thus making it a predictable, abundant food supply that especially female feral pigeons preferred to fly to (Rose *et al.*, 2006). With the closing of the Rhine Port, the population lost its main food source within a few days. This unique occasion allowed an investigation of the effect of a sudden food shortage on the reproductive success and population dynamics of this well-known feral pigeon colony under natural, urban conditions.

The results show that the number of actively breeding pairs was reduced after food limitations occurred. Pairs that continued breeding during food scarcity produced significantly fewer clutches per year with a significantly longer average clutch interval. The number of eggs per brood remained largely stable, possibly due to the low energy input required. The expectations that the hatching success would decrease, because the pigeons possibly had to spend more time on foraging, were proven wrong. Instead, the hatching success remained more or less constant under food scarcity. This observation can possibly be explained by a density dependent effect. The reduced number of active breeding pairs leads to a reduction of territorial conflicts, which is one of the main causes of egg loss (Haag, 1991). Fewer active breeding pairs imply less territorial fighting, which in turn leads to an increased chance of a squab to hatch because the possibility of an egg getting destroyed is reduced. Moreover, a significantly reduced fledgling success was monitored, most likely because the feeding of the young is the most energy demanding part of the reproductive cycle for the food-stressed adults. During the first few days, the nestlings are exclusively fed with crop milk. This represents a decisive advantage over other bird species that have to forage for specific hatchling food. As a result of the highly nutritious crop milk, pigeon squabs have a uniquely high growth rate. There is no parallel among the young of animal species studied so far to the 22-fold increase in body weight in the first three postnatal weeks as seen in pigeon squabs (Shetty *et al*., 1992). The feeding of the quickly developing young, however, comes with an increased energy input and enormous resource requirements for both parents. An adult rearing a 10 days old nestling consumes 243% of the average daily food intake of a non-incubating single adult pigeon (Riddle and Braucher, 1934). The energy requirements of two fast growing squabs are difficult to meet, which consequently leads to a high mortality rate of the young, especially under food shortage conditions. Thus, the capability of a nestling to fledge depends on the amount of food available to the parent birds.

The crucial point that leads to a reduced number of fledged young turned out to be the significantly greater number of nestlings that die during the costly rearing phase.

Consequently, a reduction in colony size is possible if immigrating birds cannot compensate the reduced number of fledged young. This subject is of great interest for biologists, especially for those working in pest management, since feral pigeons can cause severe health and economic problems in urban habitats. Estimates of pigeon demographic parameters and of their variability are crucial when selecting a suitable control strategy because they provide a working basis for determining the feasibility of attaining control (Giunchi *et al.*, 2012). The fact that a food shortage hits the breeding cycle of feral pigeons at the upbringing phase of the nestlings is important when looking at the anthropogenic food basis of the birds. As few pigeon feeders often maintain large populations, the abrupt loss of these food bases, e.g. initiated by the decease of a feeding person, have exactly the consequence that we could observe during this study: death of the young birds before the population slowly adapts to the reduced food basis. This effect could also be observed in Lausanne, Switzerland, when a wealthy pigeon mother suddenly died. The women fed the pigeons of Lausanne in great quantities. The amount she provided alone could sustain a couple of thousand pigeons. When the pigeon mother died, the populations of Lausanne had to adapt to the reduced food basis quickly (Cuendet, 2012). Thus, artificial maintenance of large feral pigeon populations, by providing large anthropogenic food bases, never represents an appropriate handling of the birds in the sense of animal welfare.

Overall, this study could demonstrate that food shortage reduced the total number of fledged young by more than half, which consequently led to a decreased colony size. However, except for the number of broods per pair, all studied reproduction parameters showed an increase in the fourth year of food scarcity. It is conceivable that the pigeons initially suffered from the sudden food loss, but eventually managed to compensate it over time by finding food elsewhere.

Additionally, it would have been beneficial to integrate another breeding colony as a control. However, the GPS proven data of the foraging places only exist for the colony in the experimental loft and were obtained within the framework of the aforementioned pre-study performed by Rose *et al.* (2006). Any assumptions of where other colonies foraged are based on few visual observations only. These observations indicate that the feeding places of the other feral pigeon breeding colonies of Basel are more dispersed. Most of the colonies feed in the city center, which is why they depend even more on intentional feeding by humans. In addition, those feeding grounds strongly vary with the season and can thus not be compared to the Rhine Port, where tons of grains represented a predictable abundant food supply all year.

In order to deal with this problem, the four years before port closure were used as a control while the four years after closure served as the analyzed data showing the effect of food loss on reproduction.

Chapter 5 gives insight of the host finding in the pigeon tick *A. reflexus*. It describes the testing of different host related stimuli and how the pigeon tick reacted towards them. The ectoparasite usually feeds on pigeons, but also enters dwellings to bite humans if their natural hosts are not available. With the growing feral pigeon populations in urban areas, their parasites also pose a growing threat to humans living in close coexistence with the birds. Feral pigeons can transmit multiple parasites, but the pigeon tick *A. reflexus* is the most important health menace from them (Haag-Wackernagel, 2005) due to its potential to trigger severe allergies. In predisposed persons, repeated bites can possibly even lead to an anaphylactic shock with fatal outcome (Buczek and Solarz, 1993). Contrary to an infection with a microorganism that needs close contact to the birds or their excreta, an *A. reflexus* bite mostly occurs without the victims's knowledge. The ticks enter human dwellings at night and bite their human hosts in their sleep. Due to this risk, it is important to understand how *A. reflexus* finds its hosts in order to disable its transmission route.

At the beginning of this study, we expected the parasite to locate a host over great distances. However, after a series of disappointing preliminary tests, including all developmental stages unsuccessfully searching a host over distances of about 30 cm, we chose to approach the problem from another perspective. As larvae have the shortest survival time without a blood meal and thus depend the most on host finding behaviour, the following experiments were exclusively performed with larval stages. Additionally, the distance between the larva and the tested host stimulus was reduced to less than 10 cm. During our laboratory tests, heat turned out to be the main stimulus that guides *A. reflexus* to its host. In hematophagous parasites, heat is a common stimulus. In accordance with the laboratory results, other studies have shown in the past that some parasites are sensitive to temperature changes as cues to detect a potential host and that heat is perceived only at very close range (Howell, 1975; Webb, 1976; Kilpinen and Mullens, 2004). As the surface temperature of a warm-blooded host drops down quickly when moving only centimeters away from it, a heat-attracted parasite consequently finds its host only at very short distances of a few centimeters. When the crucial heat stimulus was tested under natural conditions in the pigeon loft, a heated pigeon model represented a warm-blooded host. Results demonstrated that the hungry ticks were strongly attracted to the heat source. Though we only evaluated the number of larvae in our study, numerous nymphs and adults were caught as well. This observation further demonstrates that our model also works on different developmental stages of *A. reflexus*.

In conclusion, the study could show that the main stimulus that guides *A. reflexus* to its hosts is heat. However, the heat stimulus functions only over short distances. Movements of the tick seem to be initially random until right before an actual warm-blooded host is encountered. A long-distance host perception in *A. reflexus* was, at least with the here tested stimuli, not observed. The pigeon tick only comes out of its place of retreat when host encounter chances are very high, which further indicates that a pronounced host-finding behavior is simply not necessary in this species. Within the caves where the pigeons usually live, stimuli accumulate and are therefore hardly present in a gradient that could possibly guide the ticks to a blood meal. Instead, they have adapted another feeding strategy: *A. reflexus* only invests its energy resources when the effort is worth it and a host is extremely close, which is signaled by a temperature increase. It seems like the pigeon tick owes its ecological success not to its host-finding behavior, but to its extraordinary physiological features, as e.g. long life expectancy (Dautel and Knülle, 1997a), long-term starvation capability (Dautel *et al.*, 1999), high tolerance of temperature extremes (Dautel and Knülle, 1996; Dautel and Knülle, 1997b) and the capability of replenishing net water losses through absorption of water vapor from the atmosphere at relative humidities ≥ 75 % (Kahl, 1989; Dautel, 2001).

In the frame of this study, the information gained under laboratory conditions were applied in practice by installing heated pigeon models in the pigeon loft, as well as in an infested apartment. Though the information of the patient living in the infested apartment was excluded from the published manuscript, it is mentioned here as it points out the medical importance of *A. reflexus*. The 27-year-old male living in the infested apartment had previously been bitten several times by *A. reflexus* and reportedly showed strong reactions to the bites of the ectoparasite. A basophil activation test and skin prick test revealed that the patient was severely allergic to bites of the pigeon tick. He had developed an IgE-mediated allergy against *A. reflexus*, confirmed by the Clinic of Allergy of the University Hospital of Basel. When the heated pigeon models were installed in the apartment and a pigeon tick was caught on the adhesive tape surrounding one of the models, evidence was supplied that *A. reflexus* was still living in the vicinity of the patient. Due to the persistent risk of strong allergic reactions, the patient was told to avoid his apartment until disinfestation had taken place, especially during the night when the tick is active. The results of our laboratory experiments were thus integrated in this case study and were of practical use for the patient. After our examination took place, he had scientific proof of pigeon ticks infesting his living space, which finally made him decide to temporarily move out of his apartment until a disinfestation had been performed.

In the future it would be of interest to develop a ready-to-use pigeon tick trap, e.g. for pest control services. With the help of these traps, it is possibly easier to prove an *A. reflexus* infestation. Medically, one of the main problems for pigeon tick patients is that they do not know what causes their discomfort or even severe allergies. It is thus difficult for doctors to treat their patients. Most of the time, the link between detected health limitations to an ectoparasite originating from feral pigeons roosting close by is not clear. After a blood meal, the nocturnal tick quickly disappears to its place of retreat and leaves no hints except for the inexplicit health reactions of its victims. This missing link could be provided in the future by a pigeon tick trap verifying the *A. reflexus* infestation of a patient's apartment. After an infestation of the apartment has been confirmed, an allergy test of all inhabitants should be recommended to guarantee an appropriate and personal risk assessment. Additionally, pest control companies could install such heated ready-to-use traps in lodgings as a control of success after disinfestation had taken place.

Facing the increasing worldwide feral pigeon population, *A. reflexus* has to be carefully monitored as an emerging parasite with high pathogenic potential. Further studies, also including other developmental stages of the pigeon tick, are needed. Also, the perception of host stimuli over greater distances could be examined in the future, including other host stimuli that were not tested within the frame of this study. Additionally, it would be interesting to focus more on the clinical aspect. A study testing several dozens of people for allergic reactions after *A. reflexus* bites could give sensible insights for an appropriate risk assessment. This in turn could help to improve hygienic conditions and health protection when infestations of *A. reflexus* are confirmed.

6.2 General Conclusion

The abundant anthropogenic nutritional basis in urban surroundings allows the maintenance of large feral pigeon populations, which leads to overcrowding at breeding places. From an epidemiological point of view, these high population densities can ease the transmission from pathogenic microorganisms and parasites, such as *A. reflexus*, from one bird to another. While many wild-living species have a parasitic fauna comparable to that of feral pigeons, no other species lives as close to humans and offers that many possibilities of transmission. It is therefore important to carefully monitor these public health risks and their routes of transmission in the future.

A side effect resulting from a high population density of a pest species is that people try to protect themselves against the animals. This self-protection can be seen in numerous pigeon proofing systems installed in our cities. While new systems are regularly introduced onto the market, scientific proof of efficacy and their use from the point of view of animal welfare is lacking. This leads to systems violating animal protection, which are used in the field nevertheless. Examples for such systems are gel repellents that risk the gluing of plumage of feral pigeons and possibly other non-target birds. In addition, harmless and animal friendly proofing systems might become dangerous to the birds over time if they are not correctly installed and regularly maintained. It is therefore important to scientifically test each system and promote a proper installation and maintenance guide before it is introduced onto the market, otherwise an untested system might harm the birds when uninformed homeowners use it. Moreover, homeowners risk violating the animal protection law if a system harms an animal, even if this happens with no ill intent.

Proofing systems might protect a single building from a feral pigeon infestation, but the high population density of the birds living in urban environments is simply determined by the amount of food supply. Feral pigeon populations strongly depend on food abundance for maintenance and growth (Haag, 1984). A reduction in food supply thus leads to increased temporal and energetic investments in foraging, which in turn reduces reproductive effort and consequently decreases the number of individuals if immigration is unable to compensate. If the food supply abruptly decreases, the limited resources mainly affect the nestlings. While the energetic efforts of egg synthesis and incubation are minor, the energy demands of raising a brood with two nestlings are high. The fact that a food shortage hits the breeding cycle of feral pigeons at the upbringing phase of the nestlings is essential when looking at the anthropogenic food basis of the birds. As few pigeon feeders often maintain large populations, the abrupt loss of these food bases leads to the death of the nestlings before the population slowly adapts to the reduced food supply. In the long term, artificial maintenance of large feral pigeon populations, by providing large anthropogenic food bases, thus never represents an appropriate handling of the birds in the sense of animal welfare.

In conclusion, small and healthy feral pigeon stocks should be achieved by reducing the anthropogenic food base in the urban ecosystem. This would also favor a reduced disease and parasite transmission leading to a healthier coexistence of feral pigeons and humans in urban habitats.

Chapter 7

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7 References

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Chapter 8

Appendix

8 Appendix

8.1 Pretrials for Chapter 5

The main focus of this thesis was set on the “Host finding of the pigeon tick *Argas reflexus*” (chapter 5). A number of pretrials, that should not be unmentioned, were performed before the final experimental setup was satisfying enough to answer the questions of the host finding behavior of *A. reflexus*.

One of the first pretrials was the in-vitro feeding of *Argas reflexus*. The idea was to feed the ticks under laboratory conditions to have the exact fed blood volume and a precise date when all of the different developmental stages had their last blood meal. For the in-vitro feeding of *A. reflexus*, fresh pigeon blood was collected in a glass dish and immediately anticoagulated by shaking the blood with glass beads within the dish. Then, it was heated to pigeon body temperature within a water bath. Ticks were subsequently placed within a glass cylinder of which one end was covered with parafilm in order to offer the ticks a membrane to pierce through when feeding on blood. Finally, the membrane-covered cylinder containing the ticks was places within the glass dish holding the fresh, warm pigeon blood. Unfortunately, none of the ticks used during the in-vitro feeding pretrial pierced the membrane and fed on the offered blood, which is why this method was discarded.

Due to this reason all nymphs and adults had to be excluded form the experimental trials. As the date of their last blood meal was unknown, it was impossible to guarantee that the nymphs and adults were even hungry and thus willing to react to host stimuli given their ability to survive for up to several years without food. Larvae on the other hand could be used a defined amount of days after hatching. They were definitely hungry because they needed a blood meal within a short period of time to survive and to develop into nymphs.

Several other experimental setups focused on the ability of *A. reflexus* to perceive different light stimuli. As the pigeon tick is known to be negatively phototactic, infrared and ultraviolet light were tested before dimmed light was finally used in the experimental setup. While the infrared light seemed to only slightly influence the ticks searching behavior, it heated up the experimental arena, which is why the idea of using infrared light and video taping the ticks during the experiments was finally discarded. Ultraviolet light on the other hand strongly influenced the ticks’ searching behavior. Within a few minutes, almost all ticks decided to avoid the ultraviolet light and hide under offered shaded areas. As good results were finally achieved with dimmed overhead light of less than 5 lux, the experiments were performed under these light conditions instead of infrared or ultraviolet light.

Another experimental setup included pigeon nestlings that were set inside a ventilated box. The air stream circulated from one opening of the box to a diagonal other opening. The air volume was strictly regulated by an intercalated flow meter. Following the flow meter, a gas wash bottle was integrated to offer stable air humidity. However, the exhaled breath of the pigeons further strongly increased the air humidity inside the box of up to 80%. This in turn led to the intermittent clogging of the flow meter. Moreover, it could not be denied that humidity has an impact on the ticks' searching behavior. Therefore, a gas mix imitating the hosts' exhaled air was used instead.

Over time, the arena in which the ticks were set to react to different host stimuli became more and more open, as this represented a good compromise of a near-natural habitat under closed laboratory conditions. Also, the long distances of about 30–50 cm that were used in the first experimental setups had to be strongly reduced as none of the different developmental stages reacted to the presented stimuli. The distances were optimized bit by bit until the first ticks displayed a positive searching behavior.

8.2 Additional Figures of Chapter 5

During the publication process of the manuscript "Host finding of the pigeon tick *Argas reflexus*" (chapter 5), the following figure was excluded from one of the reviewers. As we think the figure is informative and helpful for readers to understand the experimental setup and achieved results, we decided to include the figure into this appendix.

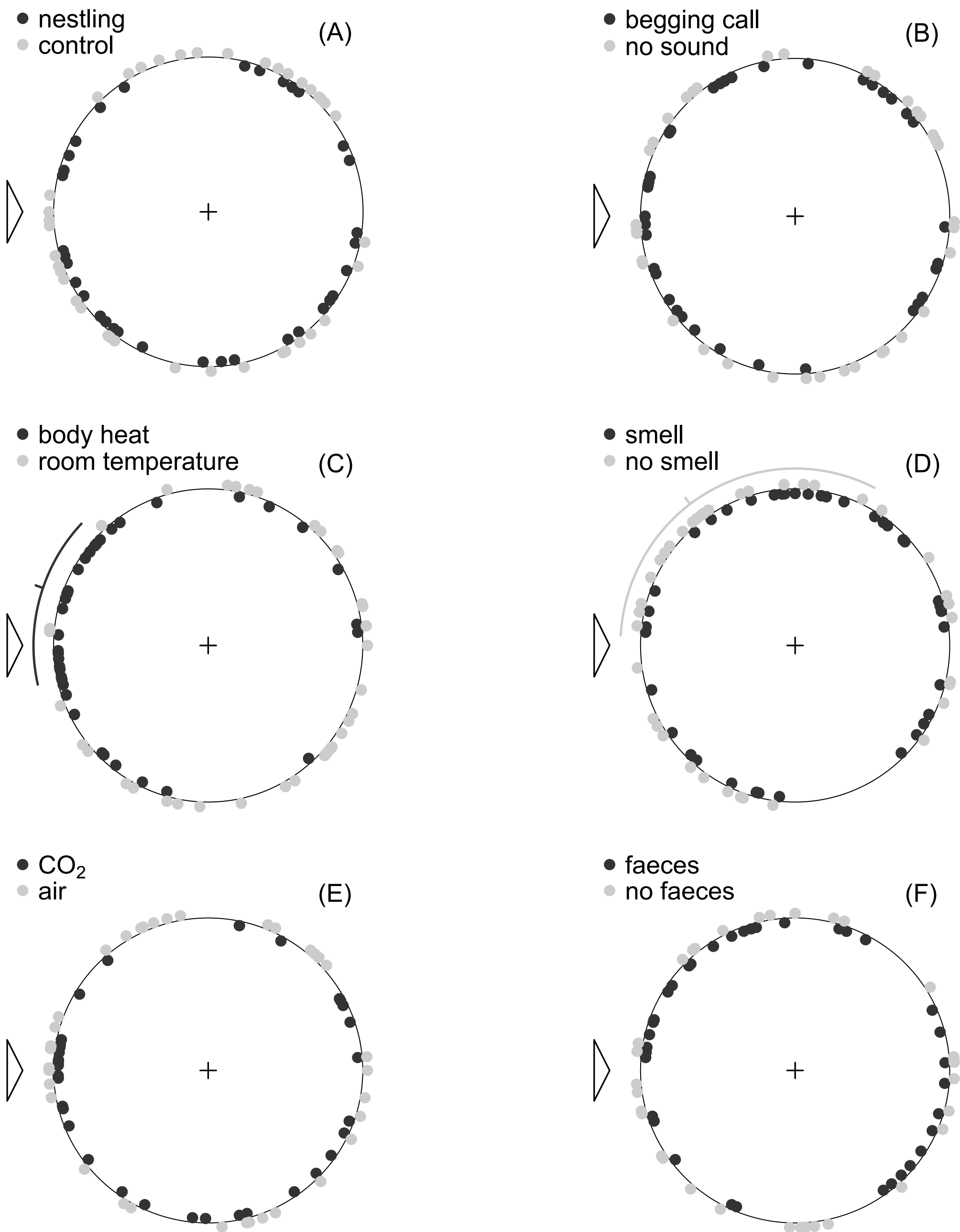

Figure 5: Movement of *Argas reflexus* larvae exposed to different host related stimuli.

The stimulus direction is symbolized with a triangle. A cross in the middle of the arena marks the starting point for the larvae. Where the Rayleigh test indicated a significant clustering of the points in one direction, marks outside the circle display the average direction (short dash) and the interquartile range (range of the central 50% of the observations).