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Author(s) :Sarah E. Bush, Scott M. Villa, Than J. Boves, Dallas Brewer and James R. Belthoff

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INFLUENCE OF BILL AND FOOT MORPHOLOGY ON THE ECTOPARASITES OF BARN OWLS

Sarah E. Bush, Scott M. Villa, Than J. Boves*, Dallas Brewer, and James R. Belthoff*

Department of Biology, University of Utah, Salt Lake City, Utah 84112. e-mail: bush@biology.utah.edu

ABSTRACT: Preening is the principle behavioral defense used by birds to combat ectoparasites. Most birds have a small overhang at the tip of their bills that is used to shear through the tough cuticle of ectoparasitic arthropods, making preening much more efficient. Birds may also scratch with their feet to defend against ectoparasites. This is particularly important for removing ectoparasites on the head, which birds cannot preen. Scratching may be enhanced by the comb-like serrations that are found on the claws of birds in many avian families. We examined the prevalence and intensity of ectoparasites of barn owls (*Tyto alba pratincola*) in southern Idaho in relation to bill hook length and morphological characteristics of the pectinate claw. The barn owls in our study were infested with 3 species of lice (Phthiraptera: Ischnocera): *Colpocephalum turbinatum*, *Kurodaia subpachygaster*, and *Strigiphilus aitkeni*. Bill hook length was associated with the prevalence of these lice. Owls with longer hooks were more likely to be infested with lice. Conventional wisdom suggests that the bill morphology of raptors has been shaped by selection for efficient foraging; our data suggest that hook morphology may also play a role in ectoparasite defense. The number of teeth on the pectinate claw was also associated with the prevalence of lice. Owls that had claws with more teeth were less likely to be infested with lice, which suggests that larger pectinate claws may offer relatively more protection against ectoparasitic lice. Experiments that manipulate the bill hook and pectinate claw are needed to confirm whether these host characters are involved in ectoparasite defense. Finally, we recovered mammalian ectoparasites from 4 barn owls. We recovered species of mammalian lice (Phthiraptera: Anoplura) and fleas (Siphonaptera) that are commonly found on microtine rodents. The owls probably acquired these parasites from recently eaten prey. This represents 1 of the few documented cases of parasites “straggling” from prey to predator.

Birds are commonly infested with ectoparasites. Ectoparasites, like ticks and lice, can vector pathogens and other parasites (Atkinson et al., 2009). Feather lice consume downy feathers; by removing these insulating feathers, birds must increase metabolic rates in order to maintain homeostasis (Booth et al., 1993). Moreover, birds that are heavily infested with lice exhibit fewer courtship displays and thus suffer reproductive costs from parasitism (Clayton, 1990; Borgia et al., 2004; Garamszegi et al., 2005). Birds defend themselves against ectoparasites in several ways. The primary defense is “preening,” in which birds use their bills to remove parasites and debris from their plumage (Rothschild and Clay, 1952). Although avian bill morphology has long been considered in terms of adaptations to improve foraging, recent work shows that some aspects of bill morphology play an important role in efficient preening (Clayton et al., 2005, 2010). Most birds have a small bill overhang, in which the tip of the upper mandible protrudes beyond the tip of the lower mandible. Comparisons among 52 species of Peruvian birds showed that species with longer overhangs had fewer ectoparasitic lice (Clayton and Walther, 2001). The effect of the overhang is also apparent within a single host species. Individual scrub jays (*Aphelocoma californica*) with overhangs have fewer lice than individuals without overhangs (Moyer et al., 2002). In rock pigeons (*Columba livia*), experimental removal of the overhang leads to drastic increases in the number of feather lice without affecting feeding efficiency (Clayton et al., 2005). Thus, the bill overhang appears to be a specific adaptation for removing ectoparasites in some species of birds. Whether extreme overhangs, such as the hooked bills of raptors and parrots, also improve preening efficiency has not been tested.

In addition to preening, birds have other behavioral defenses against ectoparasites. Scratching is an important defense against ectoparasites on the head, which is a region of the body that birds

cannot preen. Birds with foot injuries frequently have more lice than uninjured birds (Solt, 1998), which suggests that scratching may be important. Moreover, birds with long bills (such as hummingbirds and toucans) compensate for inefficient preening by scratching more (Clayton and Cotgreave, 1994). Scratching may be enhanced by the comb-like serrations that are found on the claws of some birds (Clay, 1957; Clayton et al., 2010). Pectinate claws have evolved independently in several lineages of birds; they occur in 17 different bird families, including nightjars, herons, ibis, frigatebirds, and owls (Clayton et al., 2010). The repeated evolution of pectinate claws suggests that they have some important adaptive function. To date, however, their function remains unclear.

Here we examine morphological features of the barn owl (*Tyto alba pratincola*) that may influence their ability to defend against ectoparasites by preening and scratching. Barn owls preen with their bills (Fig. 1A). Like other raptors, these owls have relatively large bill overhangs in the shape of a hook (Fig. 1B). Barn owls also scratch (Fig. 1C), and they have a pectinate flange on the middle claw of each foot (Fig. 1D) that is fully formed by the time they are 2 yr old (Johnson, 1991; Pyle, 1997). Clayton et al. (2010) included preliminary data indicating that the number of lice on barn owls is not correlated with pectinate claw morphology. However, their analyses did not consider microhabitat preferences of the different species of lice on barn owls. Lice that are found primarily on the head may experience very different selection pressures than body lice, which are found on other parts of the bird (Bush et al., 2010). For instance, since birds cannot preen their own heads, scratching may be especially important for the control of head lice, whereas preening and scratching may both be important for the control of body lice.

In the present study, we examined how beak and claw morphology relates to the prevalence and intensity of the different types of lice on barn owls. Barn owls are commonly infested with species of *Colpocephalum* and *Kurodaia*, which are “body” lice that roam all over the host. Barn owls are also infested with species of *Strigiphilus*, which are restricted to the host’s head (Price et al., 2003; Bush et al., 2010).

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*Department of Biological Sciences and Raptor Research Center, Boise State University, Boise, Idaho 83725.

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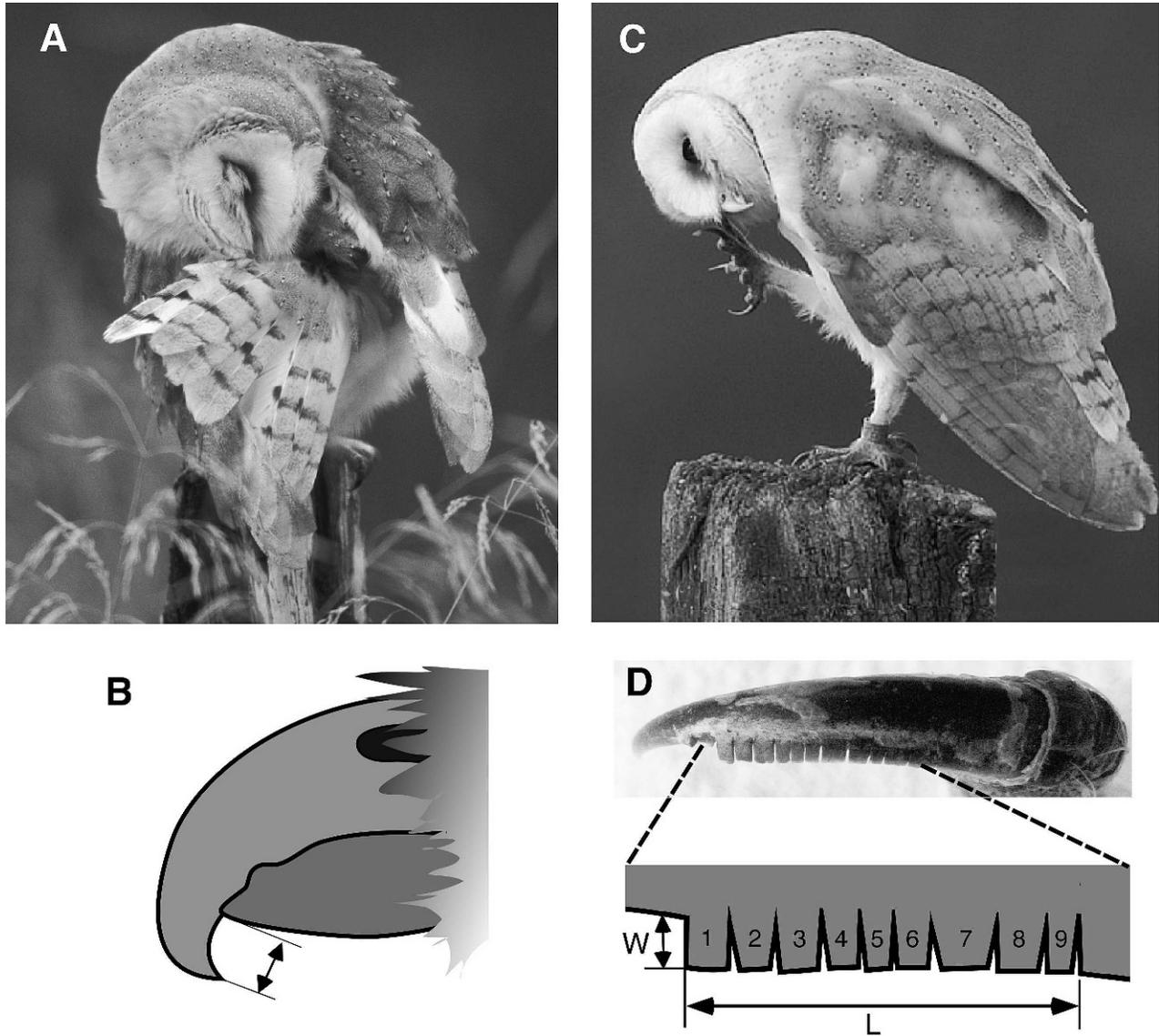


FIGURE 1. (A) Barn owl (*Tyto alba*) preening. (B) Bill hook, arrows indicate hook length measurement. (C) Barn owl scratching. (D) Pectinate claw from the middle toe of a barn owl, inset shows pectinate claw width (W), length (L), and number of teeth (9). Photos by Peter Cairns, rspb-images.com (A), and Major Wildlife, www.majorwildlifestudio.com (C).

MATERIALS AND METHODS

Barn owls in the present study came from a concurrent study focused on factors associated with highway mortality of raptors in southern Idaho (Boves, 2007). Roads were surveyed for dead barn owls twice per mo along a 248-km portion of Interstate 84 (I-84) between July 2004 and June 2006. The survey route extended from Boise, Idaho (43.6°N, 116.2°W), to Burley, Idaho (42.5°N, 113.8°W). Carcasses were collected, placed individually in plastic bags, and frozen for later processing. Only relatively fresh carcasses were used in this study, as owls in advanced stages of decomposition and owls that were severely damaged from repeated auto collisions were not collected.

In the laboratory, owls were thawed and the following data recorded: (1) gender, which was based on plumage coloration (Pyle, 1997); (2) body size, i.e., tarsus length and wingchord length; (3) bill hook length (mm), which was measured as the distance from the tip of the upper mandible to the tip of the lower mandible when the bill was closed (Fig. 1B); and (4) pectinate claw length (mm), width (mm), and number of teeth (Fig. 1D).

Ectoparasites were quantified using the Clayton and Drown (2001) body-washing technique. As some of the birds were in early stages of decomposition, many feathers and pieces of tissue were dislodged from

the carcasses during washing. To facilitate the recovery of ectoparasites, everything that was dislodged during washing was subsequently dissolved in KOH. This procedure dissolves most organic matter, but it does not dissolve the chitinous exoskeletons of ectoparasitic arthropods (Clayton and Drown, 2001). Ectoparasites were preserved in 95% ethanol for subsequent identification. Louse prevalence and intensity were determined according to the definitions in Bush et al. (1997). Statistical analyses were conducted in SAS v. 9.2 (SAS Institute, Cary, North Carolina).

RESULTS

Owl characteristics

Twenty-four barn owls were recovered. Most of the owls were female (20 females and 4 males). Tarsus length ranged from 55.0 to 90.3 cm ($\bar{x} \pm \text{SE}$: 80.7 ± 1.9 cm). Wing chord length ranged from 30.0 to 37.2 cm ($\bar{x} \pm \text{SE}$: 35.2 ± 0.3 cm). Bill hook length ranged from 3.28 to 6.22 mm ($\bar{x} \pm \text{SE}$: 4.7 ± 0.17 mm).

TABLE I. Ectoparasites found on 24 barn owls (*Tyto alba pratincola*) in southern Idaho, 2004–2006.

Typical host	Parasite type (family)	Species	Micro-habitat	Total recovered	Prevalence (%)	Intensity \bar{x} (\pm SE)
Bird	Louse (Philopteridae)	<i>Strigiphilus aitkeni</i>	Head	42	29.2	6.0 (2.0)
Bird	Louse (Menoponidae)	<i>Colpocephalum turbinatum</i>	Body	83	12.5	27.7 (25.2)
Bird	Louse (Menoponidae)	<i>Kurodaia subpachygaster</i>	Body	2	8.3	1.0 (0)
Bird	Louse (Menoponidae)	Unidentified*	Body	2	8.3	1.0 (0)
Mammal	Louse (Hoplopleuridae)	<i>Hoplopleura acanthopus</i>	—	45	12.5	15.0 (7.2)
Mammal	Flea (Ceratothylidae)	<i>Malareus telchinus</i>	—	1	4.2	1.0 (0)
Mammal	Flea (Ceratothylidae)	<i>Thrassis</i>	—	1	4.2	1.0 (0)

* These lice were either *C. turbinatum* or *K. subpachygaster* but were too damaged to identify more precisely.

Pectinate claw morphology was characterized for the 23 barn owls that had intact pectinate claws on both the right and left feet. All had pectinate claws with clearly defined teeth, which indicated that none of the individuals in this study was immature (Johnson, 1991; Pyle, 1997). We took the mean values for the pectinate claws on the left and right feet and used these means in subsequent correlation and regression analyses. One owl was missing the pectinate flange from its left foot; as it was unclear if this was natural, or if it was a consequence of post-mortem road damage, this bird was excluded from further analyses. Pectinate claw length ranged from 6.16 to 11.47 mm ($\bar{x} \pm$ SE: 9.42 ± 0.25 mm), width ranged from 0.85 to 1.59 mm ($\bar{x} \pm$ SE: 1.17 ± 0.04 mm), and the number of teeth ranged from 5.0 to 12.5 ($\bar{x} \pm$ SE: 8.1 ± 0.4).

Ectoparasites recovered

Twelve of the 24 owls (50%) were infested with lice. Three species of lice were recovered, and all of these species are known to infest barn owls (Price et al., 2003) (Table I). The head louse, *Strigiphilus aitkeni*, was the most prevalent ectoparasite species. We also found 2 species of body lice (*Colpocephalum turbinatum* and *Kurodaia subpachygaster*), which are more general in microhabitat use (Price et al., 2003) (Table I). Specimens of all 3 species of lice are deposited in PIPeR (Price Institute of Parasite Research, University of Utah, Salt Lake City, Utah).

In addition to these species of lice, 4 owls had ectoparasites commonly found on mammals (Durden and Musser, 1994). Three owls had the louse species *Hoplopleura acanthopus* (specimens deposited at Georgia Southern University, no. L-3422). One owl had the flea species *Malareus telchinus*; another owl had a badly damaged flea specimen that was probably a species of *Thrassis* (specimens deposited at the Monte L. Bean Museum, Brigham Young University, Provo, Utah). These lice and fleas were almost certainly stragglers from recently eaten rodents (see Discussion); consequently, they were not included in subsequent analyses.

Louse prevalence and intensity

Prior to analysis of prevalence and intensity, we screened for highly correlated predictor variables using Spearman's correlation analysis to avoid multicollinearity in regression models. The length of the pectinate claw was significantly correlated with the number of teeth ($r_s = 0.53$, $P < 0.01$, $n = 23$); consequently, we excluded claw length from regression analyses. As we wanted to use tarsus length as a covariate to account for potential effects of body size on parasites, we also excluded claw width from regression analyses as (1) claw width was significantly correlated to tarsus length ($r_s =$

0.46, $P = 0.03$, $n = 23$) and (2) there was no evidence from screening analyses that claw width was related to parasite prevalence or intensity. Thus, the predictor variables used in the regression analyses were tarsus length, bill hook length, and number of teeth. We ran analyses based on the prevalence and intensity of all lice, and the prevalence and intensity of head lice alone.

We examined the relationship between louse prevalence and barn owl bill and claw morphology using multiple logistic regression. The prevalence of lice was positively related to bill hook length ($B = 1.50 \pm 0.79$ SE, Wald $X^2 = 3.59$, $P = 0.06$), although this relationship was marginally non-significant. The prevalence of lice was negatively related to the number of teeth on the pectinate claw ($B = -0.66 \pm 0.32$ SE, Wald $X^2 = 4.15$, $P = 0.04$) (Table II). Odds ratios indicate that for every 1 mm increase in bill hook length, the odds of infestation by lice increased by 4.47 times (95% CI = 0.95–21.1). Odds of infestation with lice declined with each 1-tooth increase, such that they were 52% (95% CI = 27.5–97.5) of the odds at the previous step. In contrast, the prevalence of lice was not related to tarsus length ($B = 0.02 \pm 0.07$ SE, Wald $X^2 = 0.08$, $P = 0.78$). In other words, owls with relatively short bill hooks and many teeth on their pectinate claws were the least likely to be infested with lice (Fig. 2).

When analyses were restricted to head lice, we found that uninfested barn owls tended to have more teeth on their pectinate claws than infested owls (Table II: $B = -0.54 \pm 0.32$ SE, $X^2 = 2.84$, $P = 0.09$); however, the length of the bill hook was not related to whether owls were infested or uninfested with head lice ($B = 1.12 \pm 0.80$ SE, Wald $X^2 = 1.97$, $P = 0.16$). As in the case of the earlier analysis, the relationship between head louse prevalence and tarsus length was not significant ($B = -0.05 \pm 0.06$, Wald $X^2 = 0.66$, $P = 0.42$).

We examined the relationship between louse intensity and barn owl bill and claw morphology using multiple linear regression. For infested barn owls, we did not detect a relationship between (log transformed) intensity of lice and bill hook length ($B = -0.80 \pm 1.09$ SE, $|t| = 0.73$, $P = 0.49$), the number of claw teeth ($B = 0.28 \pm 0.31$ SE, $|t| = 0.91$, $P = 0.39$), or tarsus length ($B = 0.03 \pm 0.06$ SE, $|t| = 0.50$, $P = 0.63$) when considered in a multiple regression.

We ran additional analyses focused on head lice. Since the number of owls infested with head lice was relatively small, we used separate simple linear regressions in these analyses. We detected a relationship between (log transformed) intensity of head lice and tarsus length ($B = 0.08 \pm 0.02$ SE, $F_{1,5} = 16.37$, $P = 0.01$), but not bill hook length ($B = -0.86 \pm 0.82$ SE, $F_{1,5} = 1.11$,

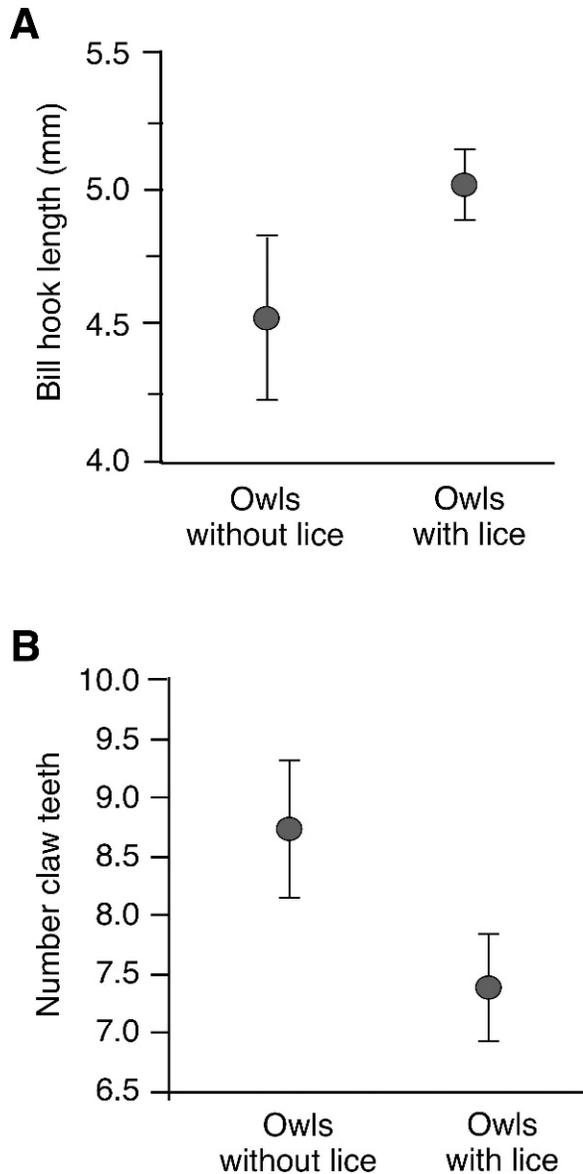


FIGURE 2. Louse prevalence as it relates to owl bill and claw morphology. (A) Uninfested owls tended to have relatively short bill hooks and (B) significantly more teeth on their pectinate claws (see Results). Bars indicate mean \pm SE.

$P = 0.34$), or number of teeth ($B = 0.21 \pm 0.31$ SE, $F_{1,4} = 0.45$, $P = 0.54$).

DISCUSSION

To investigate how owls may defend themselves from ectoparasites, we examined several aspects of bill and foot morphology that could conceivably influence the effectiveness of preening and scratching. We found that owls that were not infested with lice tended to have relatively short bill hooks (4.2–4.8 mm). When only head lice were considered, the length of the bill hook was not related to either prevalence or intensity of head lice. This is perhaps not surprising, as birds cannot preen their own heads (Bush et al., 2010).

TABLE II. Characteristics (mean \pm SE) of bill hook length and pectinate claws of barn owls with, and without, owl lice and with, and without, head lice (*Strigiphilus aitkeni*).

	All owl lice		Head lice	
	Present	Absent	Present	Absent
Bill hook				
Sample size	12	12	7	17
Length (mm)	5.01 \pm 0.13	4.52 \pm 0.30	4.99 \pm 0.17	4.67 \pm 0.22
Pectinate claw				
Sample size	11	12	6	17
Width (mm)	1.17 \pm 0.06	1.17 \pm 0.04	1.12 \pm 0.08	1.19 \pm 0.04
Length (mm)	9.08 \pm 0.40	9.72 \pm 0.30	8.99 \pm 0.44	9.57 \pm 0.30
Number of teeth	7.4 \pm 0.4	8.7 \pm 0.6	7.2 \pm 0.6	8.4 \pm 0.5

For barn owls, short bill hooks may be the most efficient for removing and killing ectoparasites on the body that are typically controlled by preening. Clayton et al. (2005) showed that the presence of a bill overhang was critical for effective preening in rock pigeons, but they also showed that bigger was not always better. They found that broken bills happened most frequently among the birds with the longest overhangs. In a study investigating the relationship between louse intensity and bill overhang morphology in western scrub jays, Clayton et al. (2010) found that jays with intermediate-sized overhangs had the fewest lice. We investigated the relationship between bill hook length and louse intensity among barn owls. We found no significant relationships between bill hook length and louse intensity, despite the fact that louse prevalence tended to be correlated with bill hook length.

The apparent discord in the relationships between bill hook length, louse intensity, and louse prevalence in this study could be explained by some unrelated factor. As with any comparative study, it is difficult to determine the causal relationship that is driving the observed patterns. For example, healthy raptors experience wear and tear on their bills as a consequence of killing and tearing through tough meat (del Hoyo et al., 1999). Raptors that are in poor condition may eat less, experience less wear on their bills, and thus may have larger bill hooks. Raptors in poor condition may also be more susceptible to louse infestation. In this scenario, bill hook length and louse prevalence could appear correlated, even if bill hook length is not important in removing lice. Although beyond the scope of the current observational study, an experiment manipulating bill hook length and monitoring the number of lice per bird could confirm whether the length of the bill hook is an important factor in effective ectoparasite control in barn owls.

Our data show that owls with the most teeth on their pectinate claws were least likely to be infested with lice. Large pectinate claws with many teeth may make scratching more efficient because owls can clean more of their plumage with each swipe of the claw. This could lead to the observed difference in louse prevalence if some owls were able to remove all of their lice by scratching. However, this process should lead to a correlation between the number of lice on infested owls and the number of teeth on the pectinate claw. We found no such pattern. Among infested owls, the number of teeth on the pectinate claws did not correlate with louse intensity. When analyses were restricted to

head lice a similar pattern emerged. Uninfested owls tended to have more teeth on their pectinate claws than infested owls. However, there was no significant relationship between the intensity of head lice and the number of teeth on the pectinate claws despite the fact that scratching is likely the principle method that owls use to control head lice.

Our study was limited to natural variation in the size and shape of the pectinate claw and natural variation in the number of lice. Since all of the owls in our study had pectinate claws, we were not able to address whether the mere presence of a pectinate claw aids in removing lice. A more definitive test would be to conduct an experiment where the pectinate claw is removed from some birds and their ectoparasite populations are monitored in relation to birds with intact pectinate claws. Experimental removal of the pectinate claw may lead to an increase in the number of lice per bird, just as the experimental removal of the bill overhang leads to dramatically increased louse populations on rock pigeons (Clayton et al., 2005).

Our result differs from the preliminary data reported by Clayton et al. (2010), which indicated that there was no relationship between louse prevalence and the number of teeth on the pectinate claw. Several factors may be responsible for the differences between these 2 studies. First, the logistic regressions used in our study are more powerful statistical methods for investigating data where multiple factors may simultaneously influence host-parasite relationships. Second, we chose to exclude straggling mammal lice from our analyses. Lice are relatively host specific, and many species have particular adaptations for attaching to their hosts (Reed et al., 2000). In fact, human crab lice have tarsal claws that are adept at grasping coarse pubic hair, but they cannot grasp the finer hair on human heads (Askew, 1971). Given this degree of specialization, it is unlikely that mammal lice will remain on barn owls regardless of their ability to preen or scratch. When the data from Clayton et al. (2010) were re-examined and the mammal lice (which were subsequently identified) were excluded, the results suggest a significant relationship with louse prevalence and the number of teeth on the pectinate claw (t -test, $df = 21$, $P = 0.04$). Thus, straggling lice appear to have obscured a relationship between the prevalence of owl lice and the claw morphology of their hosts. Our study highlights how important it is to know the identity of the parasites being examined to accurately interpret the data.

Our study also documents the prevalence and intensity of lice on barn owls in southern Idaho. Body lice (*Colpocephalum turbinatum* and *Kurodaia subpachygaster*) were found on nearly one-third of the owls, which is comparable to an earlier study of lice on barn owls in California (Morishita et al., 2001). We also found head lice (*Strigiphilus*) on 29% of the owls in our study, whereas Morishita et al. (2001) found head lice on only 7% of owls in California. The difference in prevalence between these studies may reflect geographic differences, which are known to occur in other bird-lice systems (Bush et al., 2009). However, the difference could also be the result of different sampling methods. The visual method used by Morishita et al. (2001) may have under-sampled lice restricted to a particular part of the bird, i.e., head lice, whereas the method of body washing and KOH dissolution used in this study likely removed lice more evenly from different parts of the bird (Clayton and Drown, 2001).

In addition to the lice already known to occur on barn owls, we also found that several owls were infested with mammal lice

or fleas. The owls probably acquired these ectoparasites from recently eaten voles, a staple prey item of barn owls (Marti et al., 2005; Boves, 2007). There are few published records of lice moving from prey to predator (Ansari, 1947; Whiteman et al., 2004; Palma and Jensen, 2005), yet these “stragglers” may play influential roles in parasite evolution. For example, an ecological phenomenon that can influence parasite macroevolutionary patterns is “host switching.” Records of parasites on the “wrong” host are evidence that parasites can, and do, disperse between host species in nature.

Even if parasites do disperse to new hosts, a successful host-switching event occurs only if the parasite can also survive and reproduce on the new host species. There may be many barriers to survival and reproduction (Bush and Clayton, 2006), but successful host-switches do occur (Southwood, 1989; Clayton et al., 2004). Indeed, there is evidence that ceratophyllid fleas have switched between bird and mammal hosts independently within several different flea genera (Tripet et al., 2002). The fleas found on owls in our study were both ceratophyllid fleas. Transfer of fleas from mammal prey to predatory birds may help explain why fleas in this family have undergone repeated host-switching events from mammals to birds over macroevolutionary time.

Prey to predator host switches may also occur among lice (Ansari, 1947; Whiteman et al., 2004; Palma and Jensen, 2005). Opportunities for dispersal, however, may not be sufficient to explain the observed patterns of host switching in lice. For example, raptors have a long evolutionary history of eating mammals. Mammals are commonly infested with sucking lice (suborder Anoplura), yet there are no known cases of anopluran lice infesting birds (Price et al., 2003). It seems unlikely that the straggling louse species in our study (*H. acathopus*, an anopluran) will ever establish viable populations on barn owls despite the fact that we have now documented straggling.

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