Natural History Note

Evolution of Cryptic Coloration in Ectoparasites

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abstract: Cryptic coloration is a classic example of evolution by natural selection. However, it has been studied almost exclusively in predator-prey systems, despite the fact that it may evolve in other groups, such as ectoparasites. The principle defense of hosts against ectoparasites is grooming behavior, which has a visual component. Host-imposed selection should lead to the evolution of background matching if it helps ectoparasites escape from grooming. Here we use sister taxa comparisons to show that avian feather lice (Phthiraptera: Ischnocera) have evolved coloration that matches the host's plumage, except in the case of head lice, which are protected from grooming. We also show covariation of parasite and host color within a single species of louse. Thus, cryptic coloration has evolved both within and between species of feather lice. Other examples of the evolution of crypsis presumably exist among the 70,000 known species of ectoparasites that collectively represent five animal phyla.

Keywords: background-matching coloration, crypsis, camouflage, lice, bird.

Introduction

Cryptic coloration is one of the most compelling examples of evolution by natural selection (Cott 1940; Ruxton et al. 2004; Stevens and Merilaita 2009). However, research on crypsis has focused almost entirely on predator-prey systems despite the fact that it may occur in other groups, such as parasites. Parasites are thought to represent more than half of the planet's biodiversity (Price 1980; DeMeeûs and Renaud 2002). Ectoparasites, which live on the host's integument, include 70,000 described species belonging to five animal phyla (Poulin 2007). Ectoparasites infest vertebrate and invertebrate hosts in terrestrial, freshwater, and marine ecosystems. A large number of potential host species have not been examined for ectoparasites, and undoubtedly a large number of undescribed species exist. The principle defense of most hosts against ectoparasites is grooming behavior, which has a visual component. Just as cryptically colored prey can avoid predation, cryptically colored ectoparasites may avoid host defense, yet this hypothesis has not been tested. Hosts and host-specific ectoparasites are straightforward systems in which to test for crypsis. This is particularly true for "permanent" ectoparasites, which pass their entire life cycle on the body of the host. In such cases, the host may represent both the selective agent and the background that its parasites are under selection pressure to match.

Avian feather lice (Phthiraptera: Ischnocera) are permanent ectoparasites that complete their entire life cycle on the body of the host (Marshall 1981). The 3–4-week direct life cycle begins with the egg, which is glued to the feathers, and then progresses through three nymphal instars to the adult stage. Feather lice feed on feathers and dead skin; the feather damage they cause has a chronic effect on the host that leads to reduced survival (Clayton et al. 1999) and mating success (Clayton 1990). Transmission of lice to new hosts occurs mainly during periods of direct contact, such as that between parents and their offspring in the nest (Clayton and Tompkins 1994). The principle defense against these parasites is preening behavior, during which birds use their beaks to kill and/or remove lice from their plumage (Clayton et al. 2005).

In this study we used sister taxa comparisons to test whether avian feather lice have evolved background-matching coloration to avoid preening. We selected lice from a diverse assemblage of birds representing 18 families in 12 orders. The lice were of two major types: "typical" lice and "head" lice. Typical lice are not restricted to any particular microhabitat on the body of the host; they show adaptations in body shape and behavior for hiding in feathers to escape from preening (Johnson and Clayton 2003). In contrast, head lice are plump, slow-moving lice that are specialized for the head and neck feathers, which birds can neither see nor preen (Johnson and Clayton 2003). Although birds sometimes allopreen one another, there is no evidence that allopreening helps control feather lice (Moyer and Clayton 2004). Instead, head lice are controlled largely by foot scratching, which does not have a

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visual component (Clayton 1991). In short, we predicted that typical lice would be under selection for background-matching coloration, whereas head lice would not be under such selection.

In this study we also tested for background-matching coloration within a single species of feather louse, *Quadraceps punctatus*, which has eight subspecies parasitizing different species of gulls in the genus *Larus*. The eight subspecies vary in overall color from nearly white to almost black, owing to patches on the head, thorax, and abdomen that vary in color and size (Timmerman 1952). This variation provided us with an opportunity to explore the possible relationship between parasite color and host color within a single species of parasite.

Methods

Evolutionarily Independent Comparisons

To quantify background matching in feather lice, we selected related pairs of bird species with light versus dark feathers (e.g., fig. 1). The bird species in each pair were members of the same family with one exception, which involved species from closely related families (Rallidae and Heliornithidae; table 1).

We used several criteria to assure that louse color was assessed in relation to the background (feather) color that lice naturally experience. We limited our selections to bird species that exhibited minimal sexual dimorphism in color. We also took the microhabitat use of the two different types of lice into account. For comparisons involving typical lice we included only bird species with fairly uniformly colored bodies. For comparisons involving head lice we included only bird species with uniformly colored heads. Birds were chosen based on illustrations in del Hoyo et al. (1992–2006), King et al. (1975), and the National Geographic Society's *Field Guide to the Birds of North America* (2002).

Once the species pairs of birds were identified, we searched museum databases to locate slide-mounted specimens of host-specific, congeneric lice from each pair of bird species. We used these pairs of lice for sister taxa comparisons, which rely on taxonomic hierarchies to generate evolutionarily independent comparisons in the absence of a phylogeny (Barraclough et al. 1998; Owens et al. 1999). We obtained 26 pairs of lice from a diverse

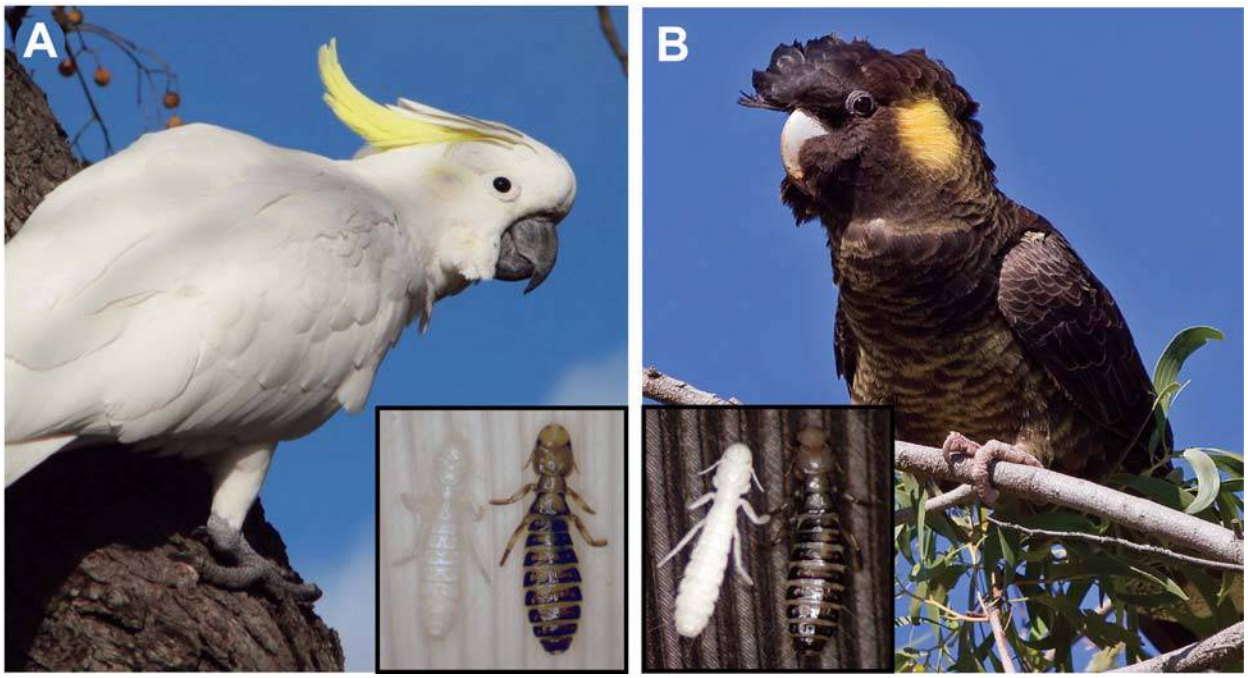

Figure 1: Example of background matching in typical feather lice. The light-colored louse, *Neopsittaconirums albus*, parasitizes the sulfur-crested cockatoo (*Cacatua galerita*; *A*). The dark-colored louse, *Neopsittaconirums borgiolii*, parasitizes the yellow-tailed black cockatoo (*Calyptorhynchus funereus*; *B*). The hosts' feathers are the natural background for these lice. Both species of lice were photographed on feathers from a sulfur-crested cockatoo (*A*, *inset*) and a yellow-tailed black cockatoo (*B*, *inset*). Cockatoo photos by Trevor Hampel (*A*) and Fir0002/Flagstaffotos (GFDL ver. 1.2; *B*).

Table 1: Pairs of light- and dark-colored bird species from which congeneric species of lice were compared

Pair	Bird family	Dark bird species	Light bird species	Louse genus	Louse form
A	Anatidae	*Cygnus atratus* black swan	*Cygnus olor* mute swan	*Ornithobius*	Typical
B	Diomedeidae	*Phoebastria nigripes* black-footed albatross	*Diomedea exulans* wandering albatross	*Episbates*	Typical
C	Diomedeidae	*P. nigripes* black-footed albatross	*D. exulans* wandering albatross	*Harrisoniella*	Typical
D	Diomedeidae	*P. nigripes* black-footed albatross	*D. exulans* wandering albatross	*Paraclisis*	Typical
E	Ciconiidae	*Ciconia abdimii* Abdim's stork	*Ciconia ciconia* European white stork	*Ardeicola*	Typical
F	Threskiornithidae	*Plegadis falcinellus* glossy ibis	*Eudocimus albus* white ibis	*Ardeicola*	Typical
G	Ardeidae	*Egretta rufescens* reddish egret	*Ardea alba* great egret	*Ardeicola*	Typical
H	Pelecanidae	*Pelecanus occidentalis* brown pelican	*Pelecanus erythrorhynchos* American white pelican	*Pectinopygus*	Typical
I	Accipitridae	*Milvus migrans* black kite	*Elanus caeruleus* black-winged kite	*Degeeriella*	Typical
J	Rallidae/ Heliornithidae	*Fulica americana* American coot	*Heliopais personatus* masked finfoot	*Fulicoffula*	Typical
K	Laridae	*Anous stolidus* brown noddy	*Sterna dougallii* roseate tern	*Quadraceps*	Typical
L	Columbidae	*Otidiphaps nobilis* pheasant pigeon	*Ducula bicolor* pied imperial pigeon	*Columbicola*	Typical
M	Psittacidae	*Calyptorhynchus funereus* yellow-tailed black cockatoo	*Cacatua galerita* sulfur-crested cockatoo	*Neopsittaconirmus*	Typical
N	Psittacidae	*C. funereus* yellow-tailed black cockatoo	*C. galerita* sulfur-crested cockatoo	*Psittoecus*	Typical
O	Cracticidae	*Cracticus quoyi* black butcherbird	*Cracticus cassicus* hooded butcherbird	*Brueelia*	Typical
P	Corvidae	*Corvus woodfordi* white-billed crow	*Corvus tristis* gray crow	*Brueelia*	Typical
Q	Diomedeidae	*P. nigripes* black-footed albatross	*Phoebastria immutabilis* laysan albatross	*Docophoroides*	Head
R	Ciconiidae	*C. abdimii* Abdim's stork	*Anastomus oscitans* Asian openbill	*Neophilopterus*	Head
S	Threskiornithidae	*Plegadis chihi* white-faced ibis	*E. albus* white ibis	*Ibidoecus*	Head
T	Accipitridae	*Milvus migrans* black kite	*Leucopternis albicollis* white hawk	*Craspedorrhynchus*	Head
U	Laridae	*A. stolidus* brown noddy	*Sterna sumatrana* black-naped tern	*Saemundssonia*	Head
V	Psittacidae	*Coracopsis vasa* greater vasa parrot	*C. galerita* sulfur-crested cockatoo	*Echinophilopterus*	Head
W	Cuculidae	*Eudynamys scolopaceus* common koel	*Scythrops novaehollandiae* channel-billed cuckoo	*Cuculoecus*	Head
X	Strigidae	*Strix nebulosa* great gray owl	*Nyctea scandiaca* snowy owl	*Strigiphilus*	Head
Y	Campephagidae	*Coracina melas* New Guinea cuckoo-shrike	*Coracina papuensis* white-bellied cuckoo-shrike	*Philopterus*	Head
Z	Sturnidae	*Sturnus vulgaris* European starling	*Sturnus malabaricus* chestnut-tailed starling	*Sturnidoecus*	Head

Note: Bird and parasite names from Price et al. (2003).

assemblage of hosts (table 1). We asked three authorities on feather lice (R. D. Price, K. P. Johnson, and V. Smith) to independently classify the lice as "typical" or "head" forms (Johnson and Clayton 2003). The results of the three authorities were in complete agreement.

We scored the luminosity of the lice as described below. Differences in luminosity were calculated by subtracting the score of the louse species on the dark-colored bird from the score of the louse species on the light-colored bird within each pair of bird species.

Luminosity Scores

We photographed microscope slide-mounted lice using a ProScope M2 camera attached to an Olympus SZ-CTV stereoscope. All photographs were taken under identical lighting conditions, and exposure was not adjusted automatically (fiber optic lighting source: Olympus Highlight 3000; 20 V/150 W, set at "normal" intensity and brightness level 3). All photos were scored digitally (Villafuerte and Negro 1998). Computer programs such as the one we used (Adobe Photoshop CS2) are calibrated for human vision; consequently, the color scores generated by such programs do not correspond perfectly to the perception of non-human animals. However, the spectral sensitivity of birds is similar to that of humans in many respects, with the most notable exception being the ability of many birds to see into the UV spectrum (Osoria and Vorobyev 2008). Because feather lice are not brightly colored, per se, nor reflect much in the UV spectrum (Kim 2008), we simply

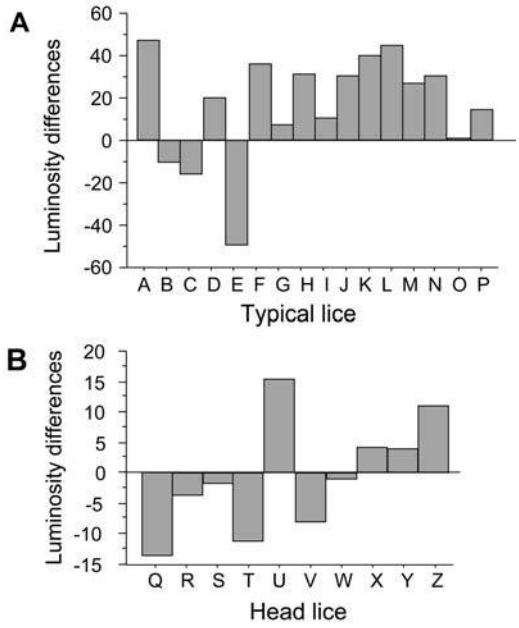

Figure 2: Differences in the luminosity scores of lice from related pairs of bird species with light or dark feathers (table 1). Positive values are cases of background-matching coloration in which the lighter louse was on the lighter host and the darker louse was on the darker host. Negative values are cases of conspicuous coloration in which the lighter louse was on the darker host and vice versa. *A*, "Typical" lice, which are not restricted to a particular microhabitat on the host, showed significantly more positive than negative differences. *B*, "Head" lice, which are protected from preening, showed no association with host color.

scored "luminosity," which is an index of the overall lightness or darkness of a subject. Using the lasso tool of Adobe Photoshop, we selected the body of each specimen (not including appendages) and recorded its mean luminosity on a scale ranging from 0 (darkest) to 255 (lightest). To correct for slight differences in luminosity due to variation in slide-mounting media, we also recorded the luminosity of a background region of the slide immediately adjacent to the specimen. We determined how much this background region differed from pure white (luminosity = 255) and then added this correction factor to the luminosity score for the louse specimen. We excluded specimens of immature lice, which are unschlerotized, as well as poorly prepared specimens and any specimens that were stained during preparation.

Subspecific Distributions in Relation to Host Color

We also examined color variation among eight subspecies of a single species of feather louse *Quadraceps punctatus*. These subspecies vary in appearance from very dark to nearly white (Timmerman 1952). Each of the eight subspecies is known to parasitize between one and six species of *Larus* gulls (del Hoyo et al. 1996; Price et al. 2003). Timmerman (1952) ranked the subspecies by color. As we were unable to obtain specimens of all of the subspecies, we simply compared Timmerman's original rankings to the color(s) of their associated host(s). To determine host color, one of us (M. Reed, who was blind to the data for lice) used color illustrations scanned digitally from del Hoyo et al. (1996) to calculate the luminosity of the different gull species. For each species, we used the lasso tool of Adobe Photoshop CS2 to select and record the mean luminosity of the shoulder and upper breast, approximating overall body color. In cases where subspecies of lice parasitize more than one species of gull (Price et al. 2003), we used the mean of the luminosity scores of the different host species.

Results

Typical lice and head lice differed in their relationships to host color. Among typical lice, 13 of 16 differences were positive, indicating that background-matching coloration has evolved more often than expected by chance in this group (fig. 2*A*; Wilcoxon signed-rank test, $P = .02$). Among head lice, which are protected from preening, louse color was not related to host color (fig. 2*B*; Wilcoxon signed-rank test, $P = .68$). The mean luminosity of typical lice from light-colored hosts was significantly greater than that of typical lice from dark hosts, as well as that of head lice from both light and dark hosts (fig. 3; Kruskal-Wallis

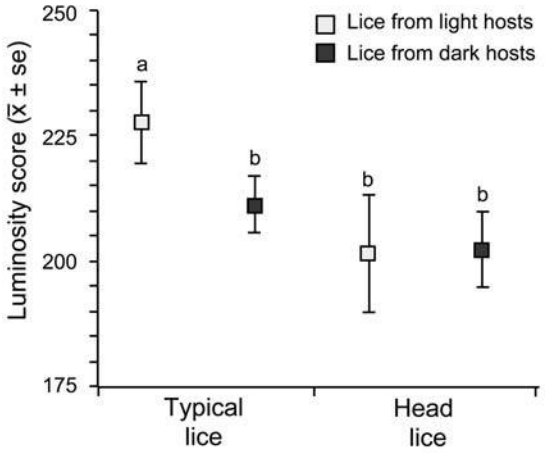

Figure 3: Luminosity scores of typical lice and head lice from light and dark hosts. Higher scores are lighter colors. Typical lice from light-colored hosts are lighter than the other three categories of lice, which do not differ from one another significantly. Different letters indicate significant differences ($P < .05$).

$\chi^2 = 11.3$, df = 3, $P = .01$). Head lice were dark colored regardless of host color; the mean luminosity of head lice from light- or dark-colored hosts did not differ significantly from that of typical lice from dark-colored hosts (fig. 3; post hoc Wilcoxon rank-sum tests, $P > .05$).

We also found evidence for background matching within a single species of louse. Color rankings of eight subspecies of the louse *Quadraceps punctatus* (Timmerman 1952) were highly correlated with our measures of host color (fig. 4; Spearman rank correlation, $\rho = 0.97$, $P < .0001$). The six nonspecific subspecies of *Q. punctatus* occurred on hosts that were more similar in color than expected by chance; the pairwise differences of luminosity scores among hosts that shared lice were significantly less than the pairwise differences between all other hosts (difference in luminosity mean ± SE: hosts of nonspecific lice 29.8 ± 2.9, all other hosts 48.6 ± 2.2; Wilcoxon signed-rank test, $P > .0001$).

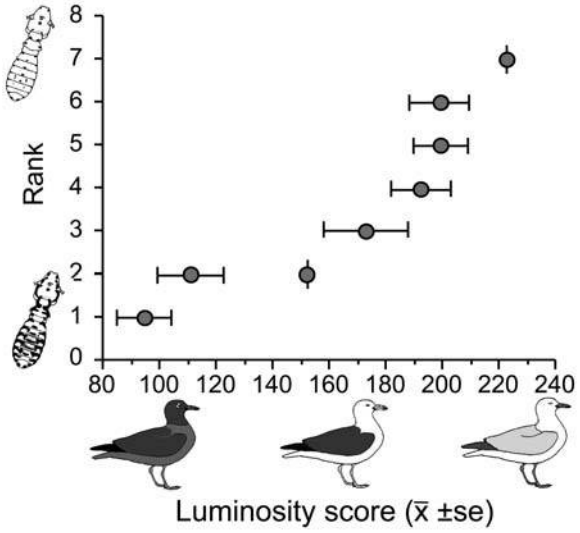

Figure 4: Relationship between color ranks (1 = darkest) of the eight subspecies of *Quadraceps punctatus* and the color of their hosts. Two subspecies of lice have a tied rank of 2. Circles with single vertical lines indicate subspecies of lice that parasitize only a single host species. Lice redrawn from Timmerman (1952).

Discussion

Our comparisons of typical lice on different-colored hosts revealed a significant relationship between parasite and host coloration, consistent with the evolution of background-matching coloration across species. In contrast, our comparisons of head lice, which are not subject to preening, showed no significant relationship between parasite and host coloration. Thus, head lice can be viewed as a kind of exception that proves the rule that preening is the selective agent responsible for background-matching coloration in typical lice. Our results further show that head lice are dark colored, regardless of host color, similar to the coloration of typical lice on dark hosts.

The tendency for head lice to be dark colored regardless of host color suggests that, in the absence of preening, dark coloration may be adaptive. Melanins, which are pigments responsible for dark coloration, are known to protect arthropods from damaging effects of UV radiation (Majerus 1998; True 2003). For example, populations of *Daphnia longispina* inhabiting clear bodies of fresh water are more melanic than populations inhabiting murky water that blocks UV penetration (Herbert and Emery 1990). The dark color of head lice could conceivably help protect them against greater UV exposure. Melanins are also involved in wound healing, cuticular hardening, pathogen resistance, and thermoregulation (Sugumaran 2002; Nice and Fordyce 2006). Further studies are needed to understand the adaptive function of dark coloration in head lice.

Our comparisons of different subspecies of *Quadraceps punctatus* from different species of *Larus* gulls also revealed a strong correlation between parasite and host coloration, indicating that background-matching coloration can occur within a single louse species. This result was somewhat surprising, given the relatively low host specificity of some of the *Q. punctatus* subspecies. Several subspecies are found on multiple distantly related *Larus* species. For example, *Quadraceps punctatus sublingulatus* is found on six distantly related *Larus* spp. (Price et al. 2003; Pons et al. 2005). The correlation between louse and host color holds, however, because nonspecific subspecies of lice are found on host species that are similar in color, regardless of their relatedness. It is unlikely that dispersal opportunities for lice between these species of gulls are correlated with host color because sympatric assemblages of *Larus* spp. typically exhibit a wide range of color (del Hoyo et al. 1996). Alternatively, the observed pattern may be the result of preening-mediated selection. By removing conspicuously colored lice during preening, birds may prevent lice from establishing populations on hosts where they are not cryptically colored. This hypothesis could be tested by comparing the survival of *Q. punctatus* that have been transferred between species of *Larus* that differ in color (cf. Bush and Clayton 2006).

The developmental or physiological mechanisms leading to the difference in color among different species and subspecies of lice is unknown. Diet is known to influence arthropod color when ingested material can be seen through a transparent body (Schmalhofer 2000) or when ingested pigments are deposited in the cuticle (Williams

et al. 1987). These "you are what you eat" strategies may be an adaptive means of providing background-matching coloration for organisms that live on the substrates that they eat. In this study, the gut contents of the lice had been cleared before the specimens were mounted on microscope slides. Therefore, the observed differences in louse color were not the result of ingested material showing through a transparent body. However, our study does not exclude the possibility that visibility of ingested feather material might further enhance the background-matching coloration of lice. Experiments conducted with typical lice from rock pigeons (*Columba livia*) show that lice reared on white and black pigeons do not differ in color (Kim 2008, unpublished data). These data suggest that it is also unlikely that differences in louse color are merely a consequence of different pigments being ingested and deposited in the cuticle.

In summary, our results suggest that background-matching coloration has evolved in feather lice in response to host preening. Other groups of ectoparasites also appear to be cryptically colored, sometimes as a result of more complicated sources of host-imposed selection. For example, the color of some species of aquatic Monogenean flatworms appears to match the color of the fish they parasitize, possibly in response to selection imposed by mutalistic cleaner fish (Whittington 1996). Other forms of crypsis may also be present among parasites, such as the parasitic crusteacean *Anilocra physodes*, which exhibits countershading (Körner 1982). It is likely that cryptic coloration has evolved repeatedly among the 70,000 species of ectoparasites known from five animal phyla (Poulin 2007). Additional studies should allow us to assess the extent to which host-mediated selection has played a role in the color diversification of ectoparasites found on a wide variety of hosts, including arthropods, fish, birds, mammals, and reptiles, all of which defend themselves using some form of grooming (Hart 1990).

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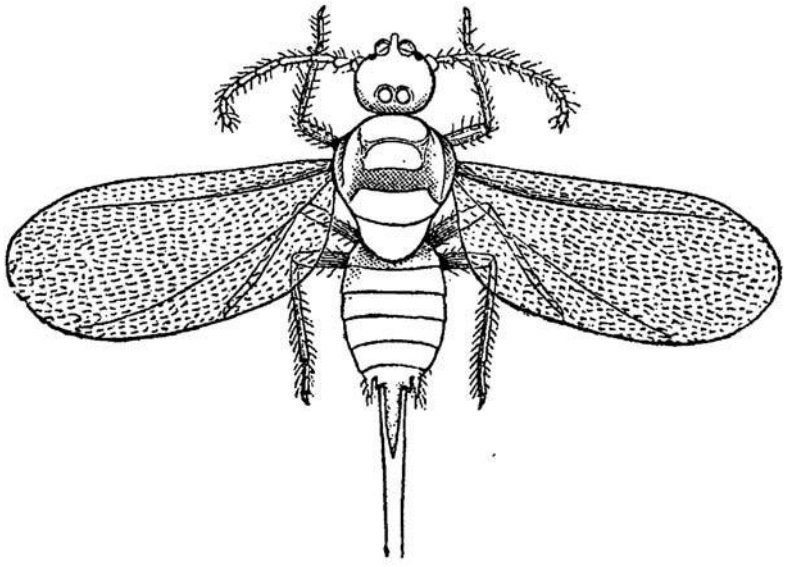

Male louse. "Comparatively few of the male-lice have as yet been discovered by entomologists, and it was with pleasure that the male of *Lecanium acericorticis* Fitch was found during the summer of 1877." From "The Maple-Tree Bark-Louse" by Emily A. Smith (*American Naturalist*, 1878, 12: 655–661).