

EVOLUTION OF TOXICITY IN PITOHUIS: I. EFFECTS OF HOMOBATRACHOTOXIN ON CHEWING LICE (ORDER PHTHIRAPTERA)

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ABSTRACT.—Birds in the genus *Pitohui* carry the potent neurotoxin homobatrachotoxin in their skin and feathers. In this study, I tested whether homobatrachotoxin can repel or kill chewing lice (order Phthiraptera). When individual feather lice were offered a choice of two feathers on which to feed or take shelter, the lice preferred nontoxic feathers to feathers of the most toxic pitohui species, *Pitohui dichrous*. Moreover, the presence of toxic *P. dichrous* feathers significantly shortened the life span of captive feather lice. These results suggest that homobatrachotoxin repels and kills lice and may thus protect pitohuis against lice infestation. Received 10 April 1998, accepted 8 February 1999.

SPECIES IN THE AVIAN GENUS *PITOHUI* carry a potent alkaloid neurotoxin in their skin and feathers (Dumbacher et al. 1992). Pitohui toxin, known as homobatrachotoxin (homoBTX), is a member of a well-known family of steroidal alkaloids that depolarize nerve and muscle membranes by binding and activating voltage-dependent sodium channels (Albuquerque et al. 1971). In some cases, concentrations of toxin are sufficiently high that merely handling an individual Hooded Pitohui (*Pitohui dichrous*) can irritate buccal membranes and can cause sneezing and burning, watery eyes (Salvadori 1881, Majnep and Bulmer 1977, Dumbacher et al. 1992). Anthropological evidence suggests that the toxin defends pitohuis from human hunters (Majnep and Bulmer 1977; Kocher-Schmid 1991, 1993), and other workers have speculated that it also defends pitohuis against natural predators (Diamond 1992) and arthropod ectoparasites (Mouritsen and Madsen 1994, Poulsen 1994). Nevertheless, no studies have directly investigated if the enemies of pitohuis are deterred by homoBTX or how homoBTX deters them.

Arthropod ectoparasites are natural enemies of pitohuis and potential targets for pitohui defensive chemicals. HomoBTX has been shown to affect a wide range of vertebrates and invertebrates (Albuquerque et al. 1971, Daly and

Spande 1986, Dwivedy 1988). With the notable exceptions of pitohuis and *Phyllobates* frogs, nearly every animal that contains voltage-dependent sodium channels is poisoned by batrachotoxins, including distantly related arthropods. Also, bird lice can influence host fitness in several ways. Lice can affect the energetics and survival of hosts (Clayton 1990, Booth et al. 1993, Brown et al. 1995), reduce egg numbers and hatching rates (Derylo 1974, DeVaney 1976), reduce mating success (Hamilton and Zuk 1982, Clayton 1990, Loye and Zuk 1991, Clayton and Tompkins 1995), and transmit pathogens (Marshall 1981, Clayton 1990). Therefore, defense against lice might be under selection. Finally, a high proportion of a pitohui's total toxin is concentrated in the skin and feathers. Because lice live and feed on feathers, skin, and subdermal blood supplies, pitohui toxins could constitute a formidable barrier to these ectoparasites.

HomoBTXs, and toxins in general, could defend birds against lice through several alternative mechanisms. Toxins could (1) reduce louse fecundity, (2) reduce louse survival, (3) reduce the influence of lice on host fitness (e.g. by delaying maturation, lengthening the life cycle, or suppressing appetite), and (4) favorably affect louse transmission rates by reducing immigration or inducing emigration. Here, I report experimental studies that examine whether feather lice exhibit an active choice against naturally toxic pitohui feathers and examine whether the presence of natural levels of

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TABLE 1. Sources and identification of chewing lice used in petri dish experiments.

Avian host species	Parasite identification	No. parasites
<i>Ailuroedus buccoides</i>	<i>Brueelia pallida</i> (Piaget, 1880)	1
<i>Alisterus chloropterus</i>	<i>Neopsittaconirmus circumfasciatus</i> (Piaget, 1880)	48
<i>Chalcophaps indica</i>	<i>Columbicola guimaraesi</i> Tendeiro, 1965	60
	<i>Coloceras piriformis</i> (Tendeiro, 1969)	74
	<i>Coloceras indicum</i> Tendeiro, 1973	5
<i>Chalcophaps stephani</i>	<i>Columbicola</i> sp.	55
	<i>Coloceras stephaniae</i> (Tendeiro, 1987)	36
	<i>Coloceras</i> sp.	20
<i>Chlamydera cerviniventris</i>	<i>Myrsidea</i> sp.	7
<i>Colluricincla megarrhyncha</i>	<i>Philoaterus</i> sp.	1
	<i>Brueelia</i> sp.	6
<i>Cuculus saturatus</i>	<i>Cuculicola latirostris</i> (Burmeister, 1838)	1
<i>Gallicolumba jobiensis</i>	<i>Columbicola exilicornis</i> (Piaget, 1880)	40
<i>Halcyon torotoro</i>	<i>Alcedoecus</i> sp.	1
<i>Macropygia amboinensis</i>	<i>Columbicola</i> sp.	3
	<i>Coloceras doreyanus</i> (Eichler, 1950)	18
<i>Melilestes megarrhynchus</i>	<i>Brueelia</i> sp.	1
<i>Pitohui cristatus</i>	<i>Myrsidea</i> sp.	1
<i>Pitohui ferrugineus</i>	<i>Myrsidea</i> sp. or <i>Philoaterus</i> sp.	7
<i>Ptilinopus magnificus</i>	<i>Columbicola harrisoni</i> Tendeiro, 1965	23
	<i>Auricotes obscurus</i> Keler, 1939	5
	<i>Hohorstiella</i> sp.	1
<i>Ptilinopus pulchellus</i>	<i>Columbicola emersoni</i> Tendeiro, 1960	1
<i>Ptilinopus superbus</i>	<i>Columbicola emersoni</i> Tendeiro, 1960	1
	<i>Auricotes pazmartinae</i> Tendeiro, 1976	5
<i>Tanysiptera danae</i>	<i>Myrsidea</i> sp.	1

homoBTX affects the captive life span of these lice.

Because toxin levels vary across pitohui species, feathers from different pitohuis provide naturally high and low toxicity treatments, and outgroups provide nontoxic control feathers. Individuals from five pitohui species are known to contain some level of homoBTX (Dumbacher 1997), with *P. dichrous* containing the highest concentrations. In some populations, *P. dichrous* feathers contain more than 50 µg of homoBTX per g of tissue, which is more than 15 times the concentration originally reported. Rusty Pitohui (*P. ferrugineus*) feathers have much lower levels, and Crested Pitohui (*P. cristatus*) feathers have nearly undetectable levels of toxin.

METHODS

Studies were conducted at the Biological Research Station, Varirata National Park (9°27'S, 147°21'E; 840 m elevation), a 400-ha reserve on the Sogeri escarpment approximately 40 km east of Port Moresby, southeastern Papua New Guinea. Birds were trapped in mist nets, measured (wing, tarsus, head and bill length, and body mass), banded, visually inspected for parasite loads, and released.

Lice were removed from host birds using fumigation jars described by Bear (1995) and equipped so industrial-grade CO₂ could be pumped constantly into the jar. Feathers were blown and ruffled to detach anesthetized lice. The lice revived within 15–30 s of exposure to normal air and then were collected in petri dishes where they were held until they could be placed into experimental arenas, usually within the hour.

In the field, lice from each individual host were classified into "types" based on body plan and body size. A type was defined as a group of morphologically similar lice taken from the same host. These louse types were later identified, and they generally corresponded to a particular species and age class (adult or immature) within that species. It was likely that each type within a particular host shared some degree of genetic and/or environmental similarity and thus, louse type provided a natural randomized block for statistical analyses. Table 1 lists all of the avian hosts that provided experimental lice and the identification of these lice to genus or species.

Experiments were performed in plastic petri dishes that contained one or two feathers and one louse. Dishes were kept at 18 to 22°C and ambient humidity (>45%) in a darkened room. In general, lice had difficulty walking across the dishes, which prevented them from escaping. In dishes with more than one feather, the second feather was placed above the first,

allowing lice to move freely from feather to feather and thereby choose from which feather to feed or rest.

All feathers were clean contour feathers in good condition taken from the dorsum just behind the wings. All non-pitohui feathers were presumed to be nontoxic. After returning from the field, toxin concentrations in pitohui feathers were measured in the Laboratory of Bio-organic Chemistry at the National Institutes of Health using radio-ligand binding assays. *Pitohui dichrous* feathers used in this study contained an average of 39 μg of homoBTX per gram of tissue, *P. ferrugineus* feathers contained an average of 3.5 μg of homoBTX per gram of tissue, whereas *P. cristatus* feathers contained less than 3 μg homoBTX per gram of tissue. Feathers collected from a variety of non-pitohui species were used as nontoxic controls.

Two types of experiments were conducted. The first set of experiments, called choice experiments, tested whether lice showed a preference against toxic pitohui feathers when given a choice of two feathers on which to feed and find shelter. The second set of experiments, called life-span experiments, tested whether pitohui toxins affected the life span of captive lice.

Choice experiments.—In the choice experiments, feathers from two bird species were placed into petri dishes, one above the other. Each petri dish contained either one pitohui feather and one non-pitohui feather, or one *P. dichrous* feather and one less-toxic pitohui feather (*P. cristatus*), matched for size and general shape. Nontoxic control feathers were used from six species: *Accipiter poliocephalus* (3 trials), *Ailuroedus buccoides* (25), *Chlamydera cerviniventris* (8), *Colluricincla megarhyncha* (49), *Dicrurus hottentotus* (5), and *Meliphaga analoga* (15). After a feather was used in an experiment, it was stored in a sealed plastic bag. Because only a limited number of feathers was available, some *P. dichrous* feathers were used in a second experiment. Of the 105 trials of *P. dichrous* feathers versus non-pitohui feathers, 23 (22%) incorporated previously used pitohui feathers. Reused feathers were always placed in fresh petri dishes and paired with a random unused feather from another species.

For the louse to choose between feathers, the design required that one feather had to be placed on top of the other and that each louse had to be placed on a feather to begin the experiment. Because lice may show an overall tendency not to move, or may prefer the bottom feather (possibly due to negative phototaxis; Marshall 1981), combinations of treatment effects (which feather the louse was placed on and which feather was on top) were distributed evenly across petri dishes. For each petri dish, feathers were randomly chosen from the two species being compared. Lice were randomly distributed to petri dishes and placed on the feather designated by

treatment design. Feathers were arranged one above the other such that lice had easy access to both feathers.

The trial began and the time was recorded when the louse was placed on one of the two feathers. Every 60 to 90 min between 0600 to 2400 Australian EST, I recorded whether the louse was alive and which feather it was on. If a louse was found alive on the dish but not on a feather, it was returned to the feather on which it had originally been placed. Each louse was monitored until it died. All lice from these experiments were preserved and stored at the Bishop Museum in Honolulu, Hawaii.

An experiment was completed when the louse was found dead in the experimental dish. All observations were tallied and a choice was recorded for the feather on which the louse was most frequently observed. In the event of a tie or if the louse was found dead in the first observation period, the dish was excluded from subsequent analysis. Choices were tabulated in contingency tables and blocked for the two design effects: (1) which feather the louse was placed on, and (2) which feather was on top. Choice experiments were conducted during November and December 1995.

Life-span experiments.—Only feathers from *P. dichrous*, *P. ferrugineus*, and *Colluricincla megarhyncha* were used. *Colluricincla*, the putative sister genus to *Pitohui*, was chosen as a control to maximize the structural similarity between *Pitohui* and control feathers. The life-span experiments used the same protocols as the choice experiments. There were three treatments (1) feathers of *P. dichrous* and *C. megarhyncha*, (2) feathers of *P. ferrugineus* and *C. megarhyncha*, and (3) a feather of *C. megarhyncha* alone. Lice in treatment 1 were therefore exposed to high natural levels of homoBTX, those in treatment 2 to low natural levels of homoBTX, and those in treatment 3 acted as controls that were not exposed to homoBTX. Data were analyzed using analysis of variance with life span as the dependent variable and treatment as the independent variable, blocked by louse type. Life-span experiments were conducted February and March 1996.

Table 2 shows the proportions of the three most common louse types used in each experiment. The proportion of different louse genera used varied between experiments.

RESULTS

Effects of toxicity on feather choice.—I performed 225 choice trials. Eleven trials ended in ties and were excluded from subsequent analyses. Lice showed a statistically significant preference for the bottom feather (G-test with Williams' correction, $G = 15.52$, $df = 1$, $P < 0.01$). Data were subsequently split into two

TABLE 2. Total number and proportion of louse genera used in choice and life-span experiments.

Genus	Total no. used	% of total
Choice experiments (214 lice total)		
<i>Coloceras</i>	116	54.2
<i>Columbicola</i>	79	36.9
<i>Myrsidea</i>	8	3.7
Other	11	5.1
Life-span experiments (208 lice total)		
<i>Columbicola</i>	103	49.5
<i>Neopsittacornirmus</i>	48	23.1
<i>Coloceras</i>	35	16.8
Other	22	10.6

blocks: petri dishes in which the louse was placed on the top feather and dishes in which the louse was placed on the bottom feather. Within each block, data were compiled into 2×2 contingency tables tallying the starting feather (toxic or nontoxic) versus the choice (stay on starting feather or move), as shown in Table 3. The two blocks were analyzed jointly using the Mantel-Haenszel one-way χ^2 statistic for blocking tables with one degree of freedom (Mantel and Haenszel 1959, Mantel 1963).

Four different treatment combinations were tested (Table 4). Lice avoided *P. dichrous* feathers in favor of nontoxic control feathers (Mantel-Haenszel statistic = 10.17, $df = 1$, $n = 105$ trials, $P < 0.0015$; Table 4). Even excluding trials with previously used *P. dichrous* feathers, lice avoided *P. dichrous* feathers in favor of nontoxic feathers (Mantel-Haenszel statistic = 5.84, $df = 1$, $n = 82$ trials, $P < 0.015$), although the level of statistical significance dropped in accordance with losing 22% of the experimental sample.

Effects of toxicity on louse life span.—Life span in captivity varied among different types of lice ($F = 3.17$, $df = 28$ and 121, $P < 0.0001$). To avoid confounding effects of treatment with effects of louse type, I used only louse types that were ex-

TABLE 3. Contingency table showing the marginal frequency distribution of all choice experiment trials. Lice are more likely to move off of a more toxic feather than a less toxic feather.

Feather on which parasite was placed	No. of lice staying on original feather	No. of lice moving to other feather or to dish
More-toxic feather	24	82
Less-toxic feather	46	62

posed to all three treatments and performed ANOVA using Type III sums of squares (Shaw and Mitchell-Olds 1993). Life-span data for 29 different louse types were analyzed for a total of 208 trials. Feather treatment (i.e. toxicity) significantly affected the life span of captive lice ($F = 5.30$, $df = 2$ and 56, $P = 0.012$).

Estimates of mean life span for each treatment are presented in Table 5. Lice exposed to feathers of *P. dichrous* or *P. ferrugineus* died significantly earlier than those living on feathers of *C. megarhyncha* (a posteriori Bonferroni *t*-tests, $\alpha = 0.05$). Life span did not differ significantly between lice exposed to feathers of *P. dichrous* versus *P. ferrugineus* ($P > 0.05$).

DISCUSSION

In the choice experiments, lice showed a statistically significant preference against feeding and resting on *P. dichrous* feathers. The ecological significance of this choice is unclear because lice rarely have an opportunity to move between hosts except during host mating and nesting periods. For many bird species, mating occurs briefly and lice have little opportunity to discriminate between hosts on the basis of toxicity. Recent evidence suggests that the most toxic pitohui species, *P. dichrous*, breeds cooperatively (Legge and Heinsohn 1996), so during

TABLE 4. Results of choice experiments. Four different treatment combinations were tested. Sample sizes for each test are given, contingency tables were blocked for effects of top and bottom feathers, and the probability of Mantel-Haenszel test statistics are presented.

Toxic feather (toxicity)	Less-toxic feather (toxicity)	<i>n</i>	<i>P</i>
<i>Pitohui dichrous</i> (high)	Nontoxic control	105	<0.001
<i>Pitohui dichrous</i> (high)	<i>Pitohui cristatus</i> (low)	36	0.373
<i>Pitohui ferrugineus</i> (low)	<i>Colluricincla megarhyncha</i> (nontoxic)	23	0.771
<i>Pitohui cristatus</i> (low)	<i>Colluricincla megarhyncha</i> (nontoxic)	50	0.354

TABLE 5. Mean life span of lice in presence of feathers of different toxicity.

Most toxic feather in petri dish	Mean life span (h)	n
<i>Pitohui dichrous</i>	35.0	74
<i>Pitohui ferrugineus</i>	41.4	67
<i>Colluricincla megarhyncha</i>	81.5	67

nesting, lice may have a choice of multiple adult and nestling hosts. Therefore, if lice can move to less-toxic individuals in the nest environment, birds without toxins may bear an unusually high lice load, and selection for antiparasite toxins could occur.

During nonbreeding seasons of avian hosts, lice may have little or no opportunity to move between hosts. Lice may still be repelled by homoBTX and drop off the host because many lice chose the dish over the toxic feather. A second possibility is that lice may be transmitted via phoresis, that is, attached to another more-mobile parasite such as a hippoboscid fly. Although phoresis is believed to be uncommon (Marshall 1981), it may facilitate transmission away from toxic hosts because hippoboscid flies were common on pitohuis (Dumbacher 1997). Alternatively, lice may migrate to areas of the bird's body that contain lower concentrations of toxin. If lice are repelled from toxic areas on an individual host, selection may favor a toxin distribution that protects regions of the body that are the most likely to be parasitized, or that pose the highest threat to host fitness.

HomoBTX profoundly increased louse mortality in the life-span experiments. Lice placed in dishes with *P. dichrous* feathers died sooner than those in dishes with *C. megarhyncha* feathers, which have undetectable levels of toxin. The life span of lice exposed to *P. ferrugineus* feathers decreased significantly compared with those exposed to *C. megarhyncha* feathers, even though toxin levels in *P. ferrugineus* feathers are about 10 times lower than those in *P. dichrous* feathers. Thus, toxin concentrations in *P. ferrugineus* and *P. cristatus* may be too low to repel lice but still may increase louse mortality.

Reducing the life span of lice can have three profound consequences for host-parasite interactions. First, any given louse will feed for a reduced period of time, reducing its individual effect on its host. Second, on average, the entire

population of lice will be smaller at any given time. Smaller populations may irritate the host less, or may be less visible to a host's potential mates. Third, if the life span of lice is reduced enough, the probability of survival to mating decreases, and subsequent generations of lice will be reduced in number.

In addition, lice that lived the longest appeared to be feeding on feathers of *C. megarhyncha*. Black powder, assumed to be fecal pellets or discarded feather bits, accumulated on the petri dishes beneath *C. megarhyncha* feathers. After 4 to 5 days, these lice had damaged a noticeable fraction of the feather. In dishes with *P. dichrous* feathers, however, lice rarely showed evidence of eating either of the feathers. In dishes with *P. dichrous* feathers, lice also became immobile and inactive. This may allow pitohuis to remove lice more easily during preening or even while flying. Given that many lice were sluggish and did not feed on pitohui feathers, pitohui toxin may also lower feeding rates and thus reduce each louse's effect. These hypotheses deserve future testing.

Life span varied significantly among louse types ($F = 3.17$, $df = 28$ and 121 , $P < 0.0001$). For the extreme examples, *Brueelia* lived an average 145 h in captivity, whereas *Coloceras* lived an average of 25 h. This difference may be due to many attributes of the different louse types, including overall differences in life span, feeding needs, previous condition, or the response to stresses of captivity. Seven lice collected from a single *Pitohui ferrugineus* host lived on average 194 h, which is the longest average captive life span of any louse type in these experiments. This may be due to homoBTX insensitivity because these lice have coevolved with toxic pitohuis. However, even these lice showed a marked difference in life span across treatments; those on *P. dichrous* feathers lived an average of 36.6 h ($n = 3$), those on *P. ferrugineus* feathers lived an average of 129.8 h ($n = 2$), and those on *C. megarhyncha* feathers lived an average of 417 h ($n = 2$). Also, the ANOVA revealed a significant interaction of treatment by louse type ($F = 1.63$, $df = 56$ and 121 , $P = 0.013$), which suggests that different types of lice react differently to the effects of homoBTX. For example, *Neopsittaconirmus circumfasciatus* showed no overall difference in life span due to feather toxicity, whereas *Brueelia* showed profound differences.

Although I collected few lice from pitohuis for this study, infestation rates in pitohuis do not appear to differ significantly from those of other muscicapids (Dumbacher 1997, R. Elbel pers. comm.).

Three caveats should be mentioned concerning my experiments. First, the experimental dishes were cooler, drier, darker, and more sedentary than a live bird's plumage. The stress of captivity may intensify effects of pitohui toxins on lice. Second, the experimental dishes may expose lice to unnaturally low concentrations of toxin. In the dishes, lice have a choice of two feathers, one of which is nontoxic. Also, because feathers contain much lower concentrations of toxin than skin (Dumbacher et al. 1992), exposure to feathers alone may underestimate the effect of natural levels of homoBTX on lice. Third, many experimental lice were collected from bird species distantly related to pitohuis. Although pitohui toxin profoundly affected these lice, the toxin may have different effects on lice that coevolved with pitohuis because parasites often evolve resistance to host defenses. However, pitohui toxins have profound effects on many species of lice, suggesting that these toxins had profound effects on pitohui lice during the evolution of toxicity in pitohuis.

It has been suggested that chewing lice have little or no influence on the fitness of their avian hosts (Rothschild and Clay 1952, Ash 1960, Marshall 1981), although recent studies suggest otherwise. Lice can reduce egg number and hatching success in chickens (Derylo 1974, DeVaney 1976), and studies of mate choice in Rock Doves (*Columba livia*) have shown that females discriminate against males with high louse loads (Clayton 1990). In addition, lice can damage plumage to the extent that thermal conductance is increased, which would increase the metabolic costs of temperature regulation (Booth et al. 1993). Even in low numbers, lice can transmit diseases that profoundly affect the fitness of their avian hosts (Clayton 1990).

Pitohui toxin may also affect other arthropod ectoparasites. Pitohui toxin attacks sodium channels composed of highly conserved proteins. These sodium channels are found in all other arthropod ectoparasites including feather mites, sucking mites, hippoboscids, soft and hard ticks, and ephemeral ectoparasites

such as chiggers, mosquitoes, and leeches. Many of these ectoparasites are believed to be more detrimental to host fitness than are feather lice. Additional studies of these other ectoparasites are needed.

This study clearly demonstrates the mechanisms by which homobatrachotoxin can defend wild pitohuis against ectoparasites. However, because homoBTX affects predators and perhaps other parasites as well as lice, it is difficult to assess the relative role of louse defense in the evolution and maintenance of pitohui toxins. Naturally occurring levels of homoBTX affect New Guinea predators such as green tree pythons (*Chondropython viridis*) and brown tree snakes (*Boiga irregularis*) and are known to deter human hunters (Majnep and Bulmer 1977, Kocher-Schmid 1991). The bright orange-and-black plumage pattern of the two most toxic pitohuis, *P. dichrous* and *P. kirhocephalus*, probably serves as an aposematic signal for visual predators such as hawks and thus would not affect lice. Consequently, homobatrachotoxin represents a single evolutionary innovation that may simultaneously influence a broad spectrum of pitohui enemies.

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