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Colonial seabird's paralytic perfume slows lice down: An opportunity for parasite-mediated selection?

Hector D. Douglas III[a,b,*]

[a] *Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, USA*
[b] *Science Department, College of Rural and Community Development, Kuskokwim Campus, University of Alaska, Bethel, AK 99559, USA*

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ABSTRACT

Selection for chemical signals in birds could be influenced by parasitism as has been previously suggested for visual and acoustic displays. Crested auklets (*Aethia cristatella*), colonial seabirds from Alaska and Siberia, offer an example of how this might occur. Crested auklets secrete lipids in plumage, possibly as an indicator of status and attractiveness. Prominent among these secretions are aldehydes, which are noticeable as a pungent citrus-like odour. Octanal and hexanal, the most abundant aldehydes in the plumage of crested auklets, are potent invertebrate repellents, reported from the chemical defenses of heteropteran insects. These aldehydes occur at high concentrations within specialized secretory structures. Experiments presented here show that these compounds can paralyse lice. Lice obtained from auklets were paralysed or killed within seconds after exposure to volatiles from nicks in the integument of a crested auklet. Chemical analysis demonstrated the presence of aldehydes in the area of integument used for this experiment. Lice exposed to control tissues in the same manner were not affected. A synthetic blend of crested auklet odourant constituents caused a sequence of impaired behaviours in auklet lice comparable to the effects of neuroactive insecticides. The time until onset of effects was dependent on dose, suggesting that the rate of molecular diffusion into louse spiracles was the explanatory factor. Impairment was evident even at very low concentrations that can occur in crested auklet plumage during winter. The same aqueous emulsions were present in both experimental and control treatments but lice in controls experiments were not affected. Crested auklets inhabit crowded social neighbourhoods with larger social groups, closer interindividual spacing and higher rates of contact than sympatric least auklets (*Aethia pusilla*). This could help to explain why crested auklets can have higher louse abundances. Lice are spread through direct contact between hosts and louse-infected mates could transmit lice to offspring. Large differences in the louse loads on crested auklet fledglings suggest differences in the parental transmission of lice to offspring.

1. Introduction

Invertebrates may use the same chemical compounds for communication and defense, but this is virtually unknown in birds. Heteropteran insects offer numerous examples of such dual functions (Blum, 1981; Aldrich, 1988). The crested auklet (*Aethia cristatella*), a colonial seabird from Alaska and Siberia, secretes chemical repellents in plumage that are also known from the chemical defenses of heteropteran insects. Octanal and hexanal, the two most abundant aldehydes in the plumage of crested auklets (Douglas et al., 2001, 2004; Douglas, 2008a) are potent invertebrate repellents reported from the chemical defenses of heteropteran insects (Waterhouse and Gilby, 1964; Blum, 1981; Aldrich, 1988; Eliyahu et al., 2012). Crested auklets are attracted to the aldehyde constituents of their citrus-like odourant (Hagelin et al., 2003; Douglas, 2008a). These compounds may be important in communication (Douglas et al., 2001, 2004; Hagelin et al., 2003; Jones et al., 2004; Douglas, 2008a; Hagelin and Jones, 2007; Hagelin, 2007). The specific composition of aldehydes could be important for signaling, particularly since two dodecenals appear to occur in a consistent 1:1 ratio (Douglas et al., 2004; Douglas, H.D., 2006. Odours and ornaments in crested auklets (*Aethia cristatella*): signals of mate quality? PhD Dissertation, University of Alaska Fairbanks, Alaska; Douglas, 2008a). Aldehydes could also help to volatilize other compounds in plumage, increasing the active space of those signals.

It has been suggested that visual and acoustic displays can serve as indicators of intrinsic quality in the signaler, if parasite load affects signal expression (Hamilton and Zuk, 1982). For example, high parasite load in male house finches (*Carpodacus mexicanus*) is correlated with reduced development of plumage coloration, a

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* Tel.: +1 907 543 4589; fax: +1 907 543 4527.
E-mail address: hector.douglas@alaska.edu

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sexually selected trait (Thompson et al., 1997). Both endoparasitic and ectoparasitic infections may affect physiological condition and impair expression of secondary sexual traits in male house finches (Thompson et al., 1997). Parasite load can also affect song performance in birds (Garamszegi, 2005).

Many species of birds are reported to emit odors (Weldon and Rappole, 1997), and it is possible that chemical signals could function as indicators of condition. For example, the crested auklet's aldehyde odourant may be derived from fatty acid metabolism (Douglas et al., 2001, 2004). Individual aldehydes occur in specialized wick feathers with their complementary fatty acid methyl ester and carboxylic acid (Douglas, PhD dissertation (cited earlier), 2008a). Fatty acids are valuable fuels and their allocation is tightly regulated (Nelson and Cox, 2004). Chemical signals are different from visual and acoustic signals in that the signal itself could have direct effects on parasites. For example, constituents of the crested auklet odourant repel or impair ticks, lice and mosquitoes (Douglas et al., 2004, 2005a,b). Gregarious social behaviour could predispose crested auklets to higher prevalence and intensity of louse infestations (Douglas et al., 2005a), and this could be a selection pressure favouring the crested auklet's aldehyde odourant. This would be consistent with what has been noted for colourful visual traits. Among birds the species that are exposed to higher levels of parasitism have more brightly coloured males (Hamilton and Poulin, 1997; Poulin and Forbes, 2012). Evolution of the crested auklet odourant could have involved mutual reinforcement by sexual and natural selection. Increased secretion of volatiles could elevate the status of the signaler while also helping to control parasites. The crested auklet's aldehyde odourant could function as a signal of mate quality (Douglas et al., 2001), because it could signal an individual's resistance against ectoparasites, its capacity to allocate endogenous resources to signal production and its attractiveness (Douglas et al., 2001, 2004, 2005b; Douglas, PhD dissertation (cited earlier), 2006, 2008a).

Aldehydes could mediate the host–parasite relationship in crested auklets and it is important to understand how the compounds are perfused in plumage. Wick feathers contain a solution with highly concentrated aldehydes (Douglas, PhD dissertation (cited earlier), 2008a). During alloanointing crested auklets appear to apply pressure on the interscapular area of a display partner with their bill, and this could forcibly expel aldehydes through translucent wick-like hairs (Douglas, PhD dissertation (cited earlier), 2008a). When aldehydes are released from secretory tissues they can volatilize rapidly, similar to the emissions of some heteropteran insects (Blum, 1981; Aldrich, 1988; Eliyahu et al., 2012). Crested auklets have dense layers of downy feathers and contour feathers; the finely branched structure of interlocking feather barbs traps air (Hanson, 2011). Volatile aldehydes can diffuse in this matrix, adsorb to surfaces of feathers, and be absorbed into oil emulsions on feathers. Hexanal and octanal partition strongly into liquid alkane emulsions (Coupland, 2006), and this phenomenon can be generalised for oils (Rabe et al., 2003a). The affinity of volatile aldehydes for lipid emulsions varies with physical state, molarity, chain length, the sequence of fatty acids and the degree of saturation (Maier, 1975; Le Thanh et al., 1992; Coupland, 2006; Rabe et al., 2003a,b). Hexanal and octanal can be rapidly excluded from emulsions (Coupland, 2006). Some studies have attempted to use plucked feathers to assay effects of plumage odors on lice (Douglas et al., 2005a; Hagelin, 2007). These authors did not report the aldehyde concentrations that were used in treatments, although they did note a citrus-like odour. A citrus-like scent might be attributable to putative oxidation products (e.g., octanoic acid). These early efforts were patterned after methods better suited for relatively inert compounds (e.g., homobatrachotoxin, Dumbacher, 1999), and a problem with this approach is that the feathers may be only a temporary substrate for volatiles. Plucking of feathers could disrupt the molecular matrix in plumage causing aldehydes to be dispersed. As a result the content of volatiles of plucked feathers may not be the same as the plumage in the integument of a living bird.

In order to understand the interaction between host and ectoparasites, it is useful to study dose response. Observations from a previous study (Douglas et al., 2004), suggested that the crested auklet odourant could have effects similar to the neuroactive substances that some terrestrial birds use for self-anointment (e.g., pyrethrum in marigolds, D-limonene in citrus, Ehrlich et al., 1986; Clayton and Vernon, 1993; Clayton et al., 2010). The hypothesis that the crested auklet odourant does not impair lice was tested. Lice were exposed to concentrations of synthetic aldehydes similar to those that can occur in the plumage of free-living crested auklets. Lice were also exposed to volatiles from the secretory tissues of a crested auklet by making a nick in the integument with the tip of a scalpel. The rationale for this experiment is that aldehydes present in secretory tissues can be released to plumage rapidly during alloanointing. While it is difficult to measure this empirically, some inferences can be made. The maximum flux of octanal that has been measured for a crested auklet at rest is 19.9 μl/50 min (Douglas, 2006). The octanal flux that can occur during alloanointing is probably greater than this. Concentrations of octanal can be 590 μg/g in plumage and up to 9.5 $\mu g/cm^2$ on accessory bill plates for crested auklets that have recently been involved in alloanointing (Douglas, PhD dissertation (cited earlier), 2008a). Furthermore, nearly pure octanal has been collected in the headspace above the napes of frozen crested auklet specimens as they thawed (Douglas et al., 2001).

Avian lice are transmitted socially (Marshall, 1981), and they could spread in a manner similar to infectious diseases. Sociality increases the opportunities for transmission of infectious diseases, because the probability of an individual becoming infected depends upon the number of agents it interacts with (McCallum et al., 2001; Ferrari et al., 2011). I adopt the term "social neighbourhood" after Ferrari et al. (2011) and others to characterise frequency- and density-dependent factors in social networks. Direct contact among birds provides lice with opportunities to move between hosts. Although it is not possible to observe the transmission of lice between birds, the frequency and number of different social contacts could be an explanatory factor for louse transmission rates. Highly connected social networks could allow lice to spread rapidly from reservoirs within the host population when conditions are favourable. Crested auklets are reported to be the most gregarious of the *Aethia* auklets (Gaston and Jones, 1998), but there are no published quantitative data to compare social neighbourhoods of crested auklet and least auklets (*Aethia pusilla*). The most observable social interactions for these species occurs on the surface of colonies during daily activity periods. This is where the largest number of birds interacts within the smallest area. These interactions may represent the greatest potential for louse transmission. Crested and least auklets attend their colonies en masse to swamp predators. They alight on landing rocks and disperse to socializing rocks and nest crevices. Generally the surface of the colony is rock talus or volcanic lava. I compared social group size, interindividual spacing, and rates of contact for crested auklets and least auklets. By social group I mean conspecifics that have the potential to come into contact due to their proximity within the colony. I tested the hypothesis that there would be no difference in these parameters with respect to species. Crested and least auklets appear to be habitual in their patterns of colony attendance. Therefore, it is reasonable to speculate that lice may spread through social networks within colonies, as has been generally proposed for wildlife populations (Ferrari et al., 2011).

Crested auklets that secrete greater amounts of aldehydes may have greater resistance against ectoparasites and transmit fewer ectoparasites to mates and offspring. Auklet chicks have few de-