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SHORT COMMUNICATION

Body size and fecundity are correlated in feather lice (Phthiraptera: Ischnocera): implications for Harrison's rule

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Abstract. 1. Harrison's rule, which predicts that large-bodied species of hosts have large-bodied species of parasites, has been documented in a wide diversity of parasites.

2. Harrison's rule has been most thoroughly studied in avian feather lice, which escape from host defence (preening) by hiding in the feathers. Lice that are unable to hide are selectively removed by preening. Preening selects for small lice on small hosts, which have small feathers in which to hide.

3. Preening should not, however, select for large lice on large hosts. Instead, the larger size of lice on large hosts is thought to result from a positive relationship between size and fecundity, as shown for many other insects.

4. This study tested for a size–fecundity correlation within *Columbicola columbae*, the host-specific 'wing louse' of rock pigeons (*Columba livia*).

5. The results confirm a positive relationship between female body length and number of eggs laid.

6. The study thus supports a mechanism consistent with stabilising selection leading to the evolution of the Harrison's rule pattern among species of *Columbicola* and their hosts.

Key words. *Columbicola*, ectoparasites, size–fecundity relationship.

Introduction

Harrison (1915) was the first to point out that large-bodied species of hosts have large-bodied species of parasites (Clayton *et al.,* 2015). This correlation, known as 'Harrison's rule', has been demonstrated in a wide diversity of parasite groups, including parasitic worms, crustaceans, fleas, flies, lice, and ticks, as well as herbivorous aphids, thrips, beetles, flies, moths, and flower mites (Harvey & Keymer, 1991; Kirk, 1991; Thompson, 1994; Sasal *et al.,* 1999; Morand *et al.,* 2000; Johnson *et al.,* 2005; Poulin, 2007). Harrison's rule has been most thoroughly documented in avian feather lice (Phthirapatera: Ischnocera), the group in which Harrison (1915) first noticed the pattern (Clayton *et al.,* 2015). More recently, Harnos *et al.* (2017) showed that Harrison's rule holds across 581 diverse species of bird lice, representing dozens of genera (Harnos *et al.,* 2017). Harrison's rule is particularly striking in the genus *Columbicola* (Clayton *et al.,* 2003; Johnson *et al.,* 2005). The number of described species of *Columbicola* has recently increased to 90, all of which are host-specific 'wing lice' that parasitise pigeons and doves (Bush *et al.,* 2009; Gustafsson *et al.,* 2015). Like other species of feather lice (Ischnocera), wing lice feed on feathers and complete all stages of their life cycle on them. The energetic cost of the feather damage caused by wing lice can lead to significant reductions in host fitness (Clayton *et al.,* 2015).

The main defence against feather lice is preening, in which birds crush or remove lice with the beak (Clayton *et al.,* 2003). Wing lice, which spend most of their time on the wings or tail, escape preening by wedging themselves in the spaces between the barbs of the large flight feathers. Lice too large to fit in the inter-barb spaces are selectively removed by preening (Clayton *et al.,* 1999, 2003; Bush & Clayton, 2006). Small-bodied species of hosts have flight feathers with narrower inter-barb spaces; correspondingly, the lice on these hosts are small enough to

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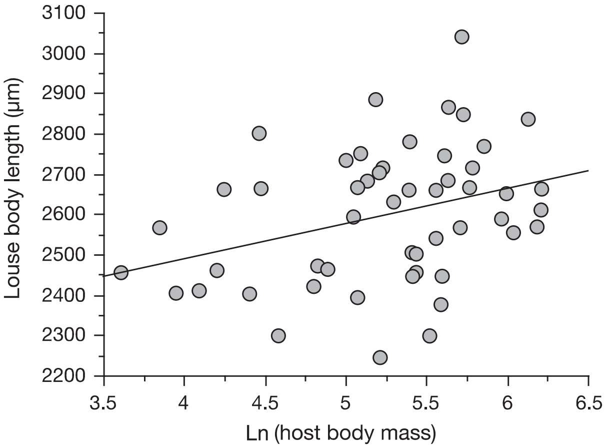

Fig. 1. Relationship between parasite body length and host body mass among host-specific wing lice (*Columbicola*) from 50 species of pigeons and doves (Table S1; linear regression; $n = 51$, $r = 0.33$, $P < 0.05$). Each point is a different host–parasite association. Parasite data were collected from one unmounted female of each species preserved in alcohol and photographed as described for live lice (see Materials and Methods). Lice were from the Price Institute of Parasite Research at the University of Utah. Host data are from Gibbs *et al.* (2001). The significant correlation between host and parasite body size is consistent with Harrison's rule, first demonstrated for *Columbicola* by Clayton *et al.* (2003) and Johnson *et al.* (2005).

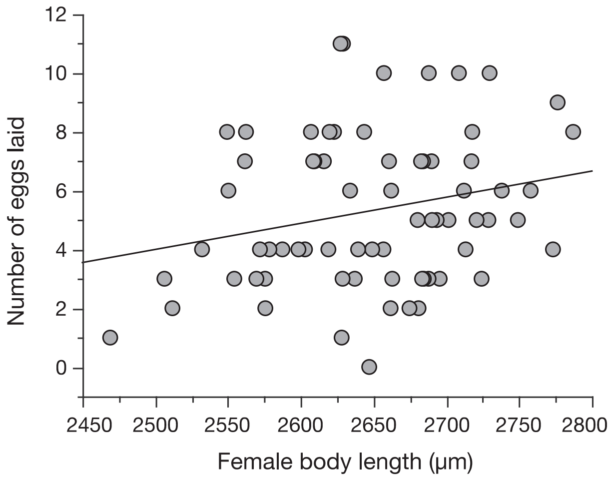

Fig. 2. Relationship between body size and fecundity in *Columbicola columbae*. Each point represents an individual live female louse. Linear regression; $n = 70$, $r = 0.25$, $P < 0.05$.

fit in the narrow inter-barb space. Bush *et al.* (2006) showed that lice placed on feathers from hosts that are larger than the typical host are capable of hiding in the wider inter-barb spaces. Thus, although preening selects for small lice on small hosts, it does not select for large lice on larger hosts. Why, then, are not all species of *Columbicola* small (Fig. 1; Table S1)? Clayton *et al.* (1999) suggested that, in the absence of preening-mediated selection, lice would evolve a larger size because larger females might lay more eggs. Here we report the results of a study in which we tested this hypothesis using *Columbicola columbae*, a host-specific wing louse of the rock pigeon *(Columba livia)*.

Materials and methods

To obtain live lice we fitted rock pigeons with harmless 'bits', which are C-shaped pieces of plastic inserted between the upper and lower mandibles of the beak (Clayton *et al.,* 1999). Bits impair the forceps-like action of the bill required for efficient preening. The result is an increase in the number of lice on birds over a period of several weeks. Bits also increase variation in the body size of lice (Clayton *et al.,* 1999), making it easier to test for a relationship between body size and fecundity.

Live female *C. columbae* were removed from pigeons using CO_2 (Moyer *et al.,* 2002), and photographed under a dissecting scope (see later). Each louse was then isolated in an 18.5-ml glass vial that contained an abdominal contour feather for food and substrate. Vials were kept in a Percival® Incubator (Perry, Iowa) set at 37 °C and 75% RH to simulate conditions on the body of the host (Bush & Clayton, 2006). Female lice were left in vials for 21 days, at which point they had stopped laying eggs. The number of eggs laid by each female was determined by one of us (YKS), who was blind to the data on louse body size.

Each louse was photographed by placing it on a glass slide with a Kodak® (Rochester, New York) Q-13 white colour standard background. A clear 22 × 22-mm glass micro-cover slip (VWR®) was placed on each louse to immobilise it while it was being photographed. This procedure does not harm lice, or distort their shape. High-resolution (2560 × 1920 pixels) digital images were taken with a DP25 digital colour camera on an Olympus SZ-CTV stereoscope (Oympus Corp., Tokyo, Japan) linked to a computer running CELLSENS image acquisition and analysis software. The body length of each louse was measured from the photograph using IMAGEJ v1.31 by one of us (MDE), who was blind to the data on louse fecundity.

Results and discussion

We processed a total of 100 female lice removed from four pigeons with impaired preening (*c*. 25 lice per bird). Thirty of the lice died during the experiment and were therefore excluded from the analysis. We quantified the number of eggs laid by the remaining 70 female lice, all of which survived the 21-day experiment. The number of eggs laid ranged between a low of 0 to a high of 11. On average (mean ± SE), lice laid one large egg (approximately 25% of the female's body length) every 5.30 ± 0.44 days, which is consistent with other studies of this species (Martin, 1934). We found a significantly positive correlation between louse body length and the number of eggs laid (Fig. 2). Thus, larger female lice have a selective advantage. In contrast, host preening will select against lice that are too large to hide in the inter-barb spaces of flight feathers. Because inter-barb space is correlated with overall host size (Bush *et al.,* 2006; Clayton *et al.,* 2015), lice on smaller hosts must be smaller to escape from preening. In summary, wing lice show a pattern consistent with stabilising selection for optimum body size for their given host.

Our study is the first to show that Harrison's rule in feather lice may be due, in part, to the positive relationship between body size and fecundity.

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SMV designed the experiment. MDE, YKS, and JCA collected the data. SMV analysed the data. SMV wrote the paper with input from SEB and DHC. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12511

Table S1. Species of *Columbicola* photographed (in alphabetical order) and their Columbiform hosts.

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