

Population density and male polymorphism in the feather mite *Falculifer rostratus* (Acari: Falculiferidae)

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Male polymorphism, in which two or more male morphologies occur within a species, is a widespread phenomenon in the Astigmata. Factors determining which morph a male will become have been studied for several free-living species. In *Sancassania berlesei* (Michael) (Acaridae), male nymphs develop into relatively unmodified homeomorphs at high population densities, and into highly modified, aggressive heteromorphs at low densities. We tested whether population density correlated with male morph ratio in the dimorphic feather mite *Falculifer rostratus* (Buchholz) (Falculiferidae). Twenty-one pigeons (*Columba livia* Gmelin) from Illinois, USA, were thoroughly washed and all *F. rostratus* extracted were identified to stage, sex, and male morph. Excluding four birds that had no *F. rostratus*, total densities per host ranged from 1-1155. Numbers of heteromorph males correlated positively with population density, but homeomorph numbers had no obvious relationship with density. Ratios of homeomorph:heteromorph were frequently higher at low population densities than at high densities – the opposite of the pattern observed for *S. berlesei*. An alternative hypothesis that quality of diet may determine morph ratio is tested and receives little support. It is possible that male morph is determined by density in *F. rostratus*, but that it is controlled at a finer physical scale (e.g., per feather) than could be measured in this study. Other possibilities are that morphs are determined genetically or by host variables we did not account for (e.g., moulting status).

Key words: Pigeon, heteromorph, homeomorph, Astigmata, population size

Male polymorphism is widespread in animals, both vertebrates (e.g., salmonid fishes) and invertebrates (e.g., scarab beetles), and is usually associated with different strategies for gaining access to females (Foote et al., 1997; Emlen 1997). Polymorphism in male mites occurs in a few Mesostigmata and Prostigmata, such as *Macrocheles* (GW Krantz, pers. comm.) and *Cheyletus* (Regev, 1974), but is most widespread and best studied in the Astigmata. The function and induction of different male morphs have been examined for several free-living species in the family Acaridae, especially in *Sancassania berlesei* (Michael). In *S. berlesei* there are two main morphs: a 'fighter' with hypertrophied legs III that are used as stabbing weapons (heteromorph), and a non-aggressive 'scrambler' with unmodified legs III (homeomorph) (Radwan, 1993; Lukasik et al., 2006). In other species of acarid there can be additional morphs (summarized in Timms et al., 1981). Heteromorphic male *S. berlesei* are aggressive and attack any other male encountered, whereas homeomorph males are non-aggressive and always lose in encounters with fighters. In this species, population density affects the development of a male into a fighter or scrambler: at low density, male nymphs become heteromorphic fighters, whereas at high density they become non-aggressive homeomorphs. The polymorphism is maintained because in small populations a fighter potentially kills all other males and monopolizes females, whereas in crowded conditions fighters spend all their time fighting rather than mating; thus scrambler males have greater reproductive fitness at high densities.

Although it has been best studied in free-living species, male polymorphism is also common in symbiotic astigmatans. In feather mites (Analgoidea, Freyanoidea, Pterolichoidea) it occurs in at least 30 genera in nine families (as calculated from illustrations in Gaud & Atyeo, 1996). Heteromorphic male feather mites frequently have enlarged

legs III or IV, but in some species it is the forelegs, palps, chelicerae or setae that are hypertrophied relative to the state in the homeomorph male. The one species of feather mite for which functions of these modifications have been studied is *Falculifer rostratus* (Buchholz) (Pterolichoidea: Falculiferidae) (Witalinski, 2004). The host for this mite is the rock pigeon *Columba livia* Gmelin (Columbidae). In *F. rostratus*, legs I and II and the lower (movable) cheliceral digits are greatly elongated in the heteromorphic male. The heteromorph is also larger in overall body size and is more heavily sclerotized than the homeomorph. Witalinski (2004) observed that heteromorphs use their elongated chelicerae and legs to lever rivals off the feather and throw them from the barb channel.

Not all male morph expression is determined by population density. In some species, polymorphism is controlled through variation in nutrition during early development. In *Onthophagus* beetles (Coleoptera: Scarabaeidae), males reared on a low-quality diet have disproportionately larger horns at any body size than males reared on a high-quality diet (Emlen, 1997). Witalinski (2004) commented on the lack of biological data for *F. rostratus* that would help to explain the occurrence of male polymorphism in this species. In this paper we tested the hypothesis that ratios of homeomorphs and heteromorphs in *F. rostratus* are associated with population density, as occurs in *S. berlesei*. We also secondarily test whether there is evidence that nutritional quality of the host, as expressed by mean body size of mites, correlates with morph ratio.

MATERIAL AND METHODS

Ninety feral rock pigeons were collected over a 1-week period in the summer of 1999 by Dale Clayton and Brett Moyer (University of Utah). Birds were captured using walk-in traps

Table 1 Characteristics of host pigeons (*Columba livia*) and numbers of different stages, sexes, and morphs of *Falculifer rostratus*, ranked from lowest to highest total number of mites.

Host characters			Counts of <i>Falculifer rostratus</i>					Total
Band no.	Sex	Body mass (g)	Hetero males	Homeo males	Adult females	Nymphs	Larvae	
801	female	305	0	0	0	0	0	0
802	male	325	0	0	0	0	0	0
813	male	340	0	0	0	0	0	0
845	male	340	0	0	0	0	0	0
810	female	295	0	0	0	0	1	1
818	male	330	0	0	0	1	0	1
807	male	390	0	0	0	1	2	3
882	unknown	160	0	0	2	2	1	5
879	female	345	7	0	13	30	8	58
839	male	315	3	0	22	33	3	61
822	female	325	4	0	22	31	10	67
851	female	320	5	4	32	35	11	87
890	male	340	4	2	39	40	9	94
842	male	275	13	3	48	54	4	122
803	male	345	5	7	38	78	10	138
876	female	305	5	14	48	69	19	155
819	female	285	33	0	115	206	64	418
884	male	380	22	14	84	283	32	435
848	male	365	27	0	130	248	55	460
859	female	345	29	27	156	357	104	673
837	male	325	90	0	315	625	125	1,155

baited with pigeon feed at locations within an 80-km radius of each other in Ford County, Illinois. Birds were humanely dispatched, and body mass and sex of each individual recorded. Body washing is a very accurate predictor of total louse abundance (Clayton & Drown, 2001), and was therefore used in this study to collect arthropods from the birds. Each pigeon was placed in a 3.8-l paint can containing a 1.0% solution of liquid dishwashing detergent. Next, the can was placed in a mechanical paint shaker (Fleming Gray, Ontario, Canada) that underwent a 10-min cycle. Upon completion, the can was opened and 95% ethanol was used to reduce the volume of foam. The bird was then deposited in a second paint can containing only water and inserted into the paint shaker for an additional 10 min. Upon completion of the second 10-min cycle, the bird was removed and rinsed over a 19-l bucket containing 95% ethanol. After sufficient rinsing, the contents of the two paint cans were poured into the 19-l bucket and rinsed several times using water to ensure that all arthropods had been removed. The contents of the bucket were then strained through a 180- μ m-mesh stainless steel screen and transferred to a Büchner funnel lined with filter paper. The filter paper was scanned using a dissecting microscope and a rough estimate of ectosymbiont numbers was made, and then the paper was placed in a wide-mouth jar filled with 95% ethanol and sealed without any arthropods having been removed from the filter paper.

For this study we selected a subsample of 21 body-washings that had a broad range of estimated *F. rostratus* numbers to allow us to test the population-density hypothesis. For the exhaustive mite counts, the filter paper was removed from the jar in approximately 4 \times 2 cm strips and placed in a 60 \times 15 mm Petri dish filled with ethanol. The contents of the dish were carefully examined using a Leica MZ16 dissecting microscope at 20-110 \times magnification. *Falculifer rostratus* specimens were removed and mounted onto microscope slides using PVA Mounting Medium (Bioquip Products, Rancho Dominguez, CA, USA). Slides were cured on a slide-warmer (ca. 40 $^{\circ}$ C) for a minimum of 3 days before they were removed. Mites were categorized as heteromorph male, homeomorph male, female, nymph, or larva using a Leica

DMLB compound microscope at 100-400 \times magnification. Linear regressions relating numbers of heteromorphs and homeomorphs to total number of mites on birds were performed using the statistics package SPSS version 11.5 (SPSS for Windows, 2002). We also tested for evidence of a correlation between body weight of host and mite number (Pearson r), and whether host sex influenced mite load (two-sample t-test).

To explore the hypothesis that the smaller-bodied homeomorph males may develop on hosts that provide poor nutrition, we selected four pigeons that had both homeomorph and heteromorph males (bird band numbers 803, 851, 859, 876) and four that had only heteromorph males (819, 837, 848, 879) (Table 1). We haphazardly selected 5-10 females and 4-11 heteromorph males per host for a total of 50 females and 50 heteromorphs (25 each from birds with homeomorphs and heteromorphs, and 25 each from those with only heteromorphs). The body length of each mite was measured ventrally from the anterior margins of epimerites I to the median indentation at the opisthosomal terminus. Mean body lengths were compared between mites from birds with both male morphs and those with only heteromorph males using a one-tailed t-test. A one-tailed test was used because the hypothesis was directional: mites from hosts with both male morphs should be smaller than those from hosts with only heteromorphic males.

RESULTS

Falculifer rostratus were found in 17 of the 21 body-washing samples (Table 1). Excluding those birds that had no *F. rostratus*, total densities per host ranged from 1-1155. Females and nymphs were always more abundant than males. Thirteen samples included heteromorphic males, and of these, seven also included homeomorphs. Body mass of host was not correlated with *F. rostratus* load (Pearson $R = 0.17$, $P = 0.46$), and there was no difference in load between male and female hosts ($t = 0.18$, d.f. = 18, 2-tailed $P = 0.87$). In addition to *F. rostratus*, we found mites from seven other families in the body washings: *Diplaegidia columbae*

(Buchholz) (Analgidae), Dermoglyphidae, Harpirhynchidae, Cheyletiellidae, Syringophilidae, *Tinaminyssus melloi* (Castro) (Rhinonyssidae), and *Dermanyssus gallinae* (De Geer) (Dermanyssidae). Three species of lice were also found: *Campanulotes compar* (Burmeister) and *Columbicola columbae* (Linnaeus) from the Philopteridae and *Hohorstiella lata* (Piaget) from the Menopodidae.

There was a significant positive relationship between total number of *F. rostratus* on a bird and the number of heteromorphic males ($r^2_{adj} = 0.92$, $P < 0.001$), but there was no relationship between density and number of homeomorphs ($r^2_{adj} = 0.042$, $P = 0.21$) (Fig. 1). When the ratio of number of homeomorphs to heteromorphs is plotted against population density (Fig. 2), there is no evidence of the predicted increase in proportion of homeomorphs with total number of mites per bird. Instead, at low densities there is wide variation in morph ratio, with homeomorphs being either more common or rarer than heteromorphs, but at higher densities the proportion of homeomorphs is low.

Mean body length of heteromorphic males from birds with both types of male morphs did not differ significantly from that of heteromorphs from birds that had only heteromorphic males ($t = 0.063$, d.f. = 48, 1-tailed $P = 0.48$) (Fig. 3A). Female body length was significantly, albeit only slightly, less on hosts with both morphs ($t = 1.84$, d.f. = 48, 1-tailed $P = 0.036$) (Fig. 3B).

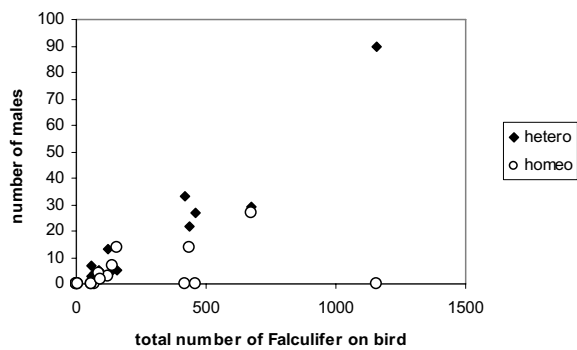


Figure 1 Relationship between total number of *Falculifer rostratus* per host pigeon and number of heteromorphic and homeomorphic males.

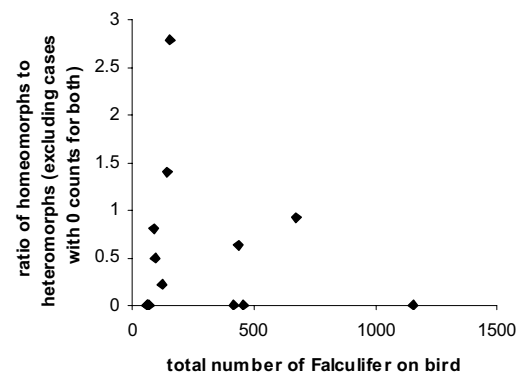


Figure 2 Ratio of homeomorphic to heteromorphic males plotted against total number of *Falculifer rostratus* per host pigeon.

DISCUSSION

We found no evidence that homeomorphic male *F. rostratus* were more likely to develop on hosts with high densities of mites. Instead, it appeared that homeomorphs declined in relative abundance at higher population densities, whereas heteromorph numbers mirrored total mite number (Fig. 1). The need to exclude cases in which there were no males at all resulted in a small sample size for the morph ratio plot ($n = 11$, Fig. 2), and therefore we are reluctant to place too much emphasis on the negative triangular shape of the distribution. Nevertheless, these data allow us to reject the hypothesis that homeomorphic males dominate at high total population densities. It is still possible that male morph is determined by density in *F. rostratus*, but that it is controlled at a finer physical scale (e.g., per feather) than could be measured in this study. This could be tested by a correlational study in which feathers are examined individually, either on living hosts or on hosts that had been frozen or plucked immediately after death (to prevent movement of mites among feathers).

It is also possible that the mechanism determining male morph is something different from that operating in *S. berlessei*. We found little evidence that the controlling factor was quality of nutrition provided by the host. Although females from birds with both male morphs were significantly smaller than those from heteromorph-only birds, as predicted by

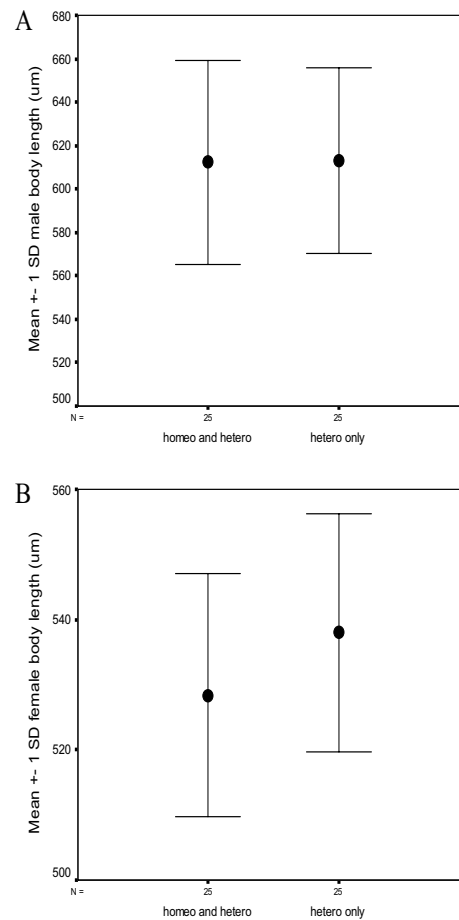


Figure 3 Mean (\pm SD) body lengths of *Falculifer rostratus* on hosts that had both male morphs, and those that had only heteromorphs: (a) body lengths of heteromorphic males; (b) body lengths of adult females.

our hypothesis, this difference was very small, and heteromorphic males did not show any difference in size (Fig. 3). It would be interesting to test the nutritional hypothesis in a controlled laboratory experiment in which the amount of preen oil provided to mites is manipulated. Other possibilities are that morphs are determined genetically or by host variables we did not account for (e.g., moulting status).

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