Zoologischer Anzeiger xxx (2018) xxx–xxx

Contents lists available at ScienceDirect

Zoologischer Anzeiger

journal homepage: www.elsevier.com/locate/jcz

Zoologischer Anzeiger

Asymmetry and polymorphism in males of the feather mite *Michaelia neotropica* Hernandes and Mironov (Acariformes: Astigmata: Freyanidae)

Heather Proctor[a,*], Wayne Knee[b]

[a] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6 2E9, Canada
[b] Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, K1A 0C6, Canada

ARTICLE INFO

Article history:
Received 3 November 2017
Received in revised form 22 January 2018
Accepted 23 January 2018
Available online xxx

Keywords:
Arachnida
Mites
Heteromorphism
Chirality
Sexual selection
Aves
Bird

ABSTRACT

Polymorphism is common among male astigmatan feather mites (Acariformes: Astigmata: Analgoidea, Pterolichoidea). The more highly modified morph (the 'heteromorphic' male) typically shows symmetrical hypertrophy of one or two pairs of legs. However, males of several genera of feather mites show an additional type of polymorphism in which some males have elaborate modifications only on the right side of the body, and others on the left. We examined male polymorphism in *Michaelia neotropica* Hernandes and Mironov, a symbiont of New World cormorants (Aves: Phalacrocoracidae), to determine the frequency of all morph types, whether some morph types more frequently co-occurred than others, and whether left- or right-handedness was associated with the particular location of the male on the host's wing. We also tested whether certain male morphs were more likely to be found with females. Of 110 male *M. neotropica* from nine culled cormorants from Alberta, Canada, 87 were homeomorphic and 23 were heteromorphic. The ratio of left- to right-handedness was exactly 50:50. There were no significant associations between homeo- and heteromorphy and left- or right-handedness. Left-handed males were most commonly found on the host's right wing, and right-handed males on the left wing. We discuss the possible function of asymmetry in these mites and suggest that left- and right-handedness is not genetically defined but rather is a product of differential stresses on muscles during a male's nymphal stages.

1. Introduction

Polymorphism is common among males of the mite group Astigmata (Arachnida: Sarcoptiformes: Oribatida). In free-living species of Astigmata, the most common type of polymorphism is for some males to have relatively slender, female-like legs (the homeomorphic state), and others to have one or more pairs of symmetrically enlarged, heavily sclerotized legs and a more heavily armoured ventral side (the heteromorphic state) (Walter and Proctor, 2013). Heteromorphic males tend to be aggressive and to use their hypertrophied legs to fight rival males for access to females (*e.g.*, Radwan et al., 2002). Polymorphism is also common among male astigmatan feather mites (Analgoidea, Pterolichoidea), in which the heteromorphic male typically shows symmetrical hypertrophy of one or two pairs of legs (Gaud and Atyeo, 1996). The function of hypertrophied appendages is more complicated to assess in feather mites, which have proven very difficult to rear off of living hosts, but modified legs are most commonly associated with holding the adult female or female tritonymph during copula or precopula. Males of several genera of feather mites show an additional form of asymmetric polymorphism in that some males have elaborate modifications only on the right side of the body, and others on the left. In certain cases, asymmetrical hypertrophy is expressed in diametrical limbs, *e.g.*, right foreleg and left hindleg, making the males appear as if they have been stretched in opposite directions (*e.g.*, Alloptidae: *Dinalloptes*, Freyanidae: *Michaelia*). Some species combine this with the more common form of polymorphism and show four possible male states: left- and right-handed homeomorphs, and left- and right-handed heteromorphs. Females and juvenile males do not show this asymmetry.

What is the function of adult male asymmetry? When departures from bilateral or radial symmetry occur at the level of male genitalia or paragenitalia such as spermatophores, there is usually a predictable direction from which the male approaches the female

* Corresponding author.
E-mail address: hproctor@ualberta.ca (H. Proctor).

https://doi.org/10.1016/j.jcz.2018.01.010
0044-5231/

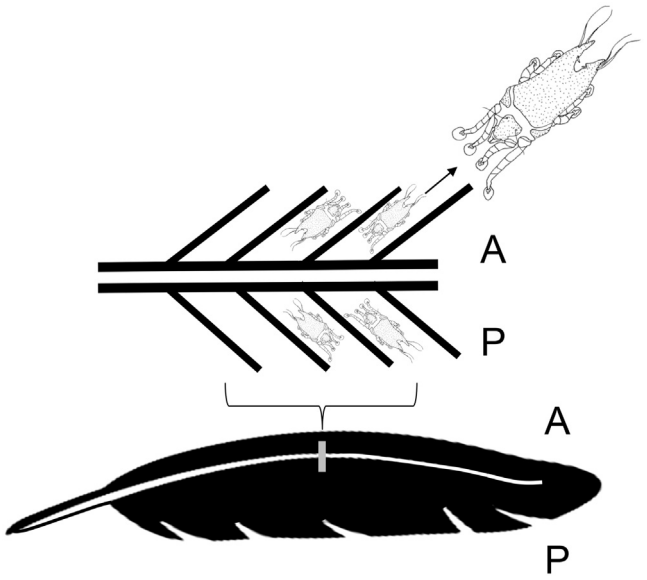

Fig. 1. Possible orientations of male *Michaelia neotropica* on flight feathers: male anterior to (A) or posterior to (P) the rachis, male's gnathosoma ('head' end) facing away from the rachis (mites on the left) or towards the rachis (mites on the right).

to copulate (Schilthuizen, 2013), or the female approaches the spermatophore to pick up sperm (Weygoldt, 1969). In asymmetrical male feather mites, however, the asymmetry is not at the genitalic level. Dubinin (1951) suggested that the asymmetrically modified legs (and sometimes entire bodies) of these males allowed them to better brace themselves in feathers while using their hind legs to hold females during copula or pre-copula. Asymmetrical males are most common in feather mite species associated with the flight feathers of aquatic birds; males on these hosts have to deal with hydrodynamic as well as aerodynamic stresses while on the feathers. What benefit might asymmetry provide in these conditions? Compared to contour feathers, the barbs and interbarb channels of flight feathers are strongly slanted relative to the rachis (Fig. 1). Where the barbs meet the rachis this produces a trapezoidal rather than a rectangular interbarb channel. Barb channels anterior to the rachis are slanted in a way that is (relatively) mirror-image to that of the posterior edge of the feather (A and P in Fig. 1). Thus, if male asymmetry is associated with microhabitat, there could be left- and right-handed mites on each wing at same time but (a) on different sides of the rachis, or (b) on the same side of the rachis, but facing different directions relative to the rachis. Alternatively, males could always be in the same position relative to the rachis but left- and right-handed males could be on different wings.

Specific details of male location are difficult to determine except under stringent criteria involving no contamination between left and right wings and quick preservation to keep mites *in situ* on feathers. We took advantage of a governmentally sponsored cull (McGregor, 2014) of Double-crested Cormorants, *Phalacrocorax auritus* (Lesson, 1831), in Alberta, Canada, to explore correlates of male morphology in one of its feather mites, *Michaelia neotropica* Hernandes and Mironov, (2016) (Freyanidae). Males of this species exhibit all four morph states. The heteromorphic male has a more heavily sclerotized venter and greater asymmetry of the terminal lobes than the homeomorph, and both hetero- and homeomorphs have either the right or left leg II longer and with a more curved tarsus than the other leg II (Fig. 2; for more illustrations, see Hernandes et al., 2016). Males hold onto nymphal or adult females using their hind legs and anal suckers, with only the anterior legs holding onto the surface of the feather. Our goals were to assess the frequency of all morph types, determine whether some morph types more frequently occurred in combination than others, and whether left- or right-handedness was associated with the particular location of the male on the host's wing.

2. Materials and methods

Field staff from Alberta Sustainable Resource Development culled double-crested cormorants (*Phalacrocorax auritus*) from Lac la Biche, Alberta, Canada (N 54.854°, W 111.987°) during the summers of 2004 and 2005. Sixteen of these cormorants were retrieved immediately after being shot, and their wings were cut off, carefully spread flat, and separately placed in labeled plastic bags. The wings were placed on ice and moved to −20 °C freezers within a few hours after collection. We retrieved the wings and took them to the University of Alberta, where they were kept frozen until processing.

Each wing was carefully examined feather by feather for male *Michaelia*. When a male was found, the following aspects were noted before the mite was removed from the feather and mounted on a microscope slide: bird specimen number, male from the left or right wing, male holding a female in copula or precopula in his hind legs, male positioned within an interbarb channel or 'loose' on the feather (indicating that the mite had been dislodged during transport), male anterior to or posterior to the rachis, male's gnathosoma ('head' end) facing towards the rachis or away from the rachis (Fig. 1). Casual observations of density of other mites on the wing were also noted.

We mounted each male mite on a separate slide in PVA mounting medium (6371A, BioQuip Products, Rancho Dominguez, California, United States of America). We placed the males consistently with their ventral sides up to facilitate determination of handedness in subsequent microscopic examination. Slides were left to cure on a slide warmer for a minimum of 4 days at ∼40 °C. We examined each male using a Leica DMLB compound microscope with DIC illumination and noted whether it was (a) left- or right-handed, and (b) homeomorphic or heteromorphic.

We combined data from all male-bearing hosts for analysis. For all males, we assessed the following: frequency of the four morph types, whether some morph combinations co-occurred more frequently than others (*e.g.*, were heteromorphs more likely to be left- than right-handed?), and whether left- or right-handedness was associated with being on the left or right wing. After excluding the males that were 'loose' on the feather, we also tested whether handedness was associated with the particular location of the male on the host's feather (anterior or posterior to the rachis, facing towards or away from the rachis) and whether particular morph types were more likely to be found holding an adult or nymphal female. We performed all tests using GraphPad's Fisher's Exact Test (https://www.graphpad.com/quickcalcs/contingency1/).

3. Results

In addition to *Michaelia neotropica*, we observed species from four other genera of feather mites: *Dinalloptes*, *Plicatalloptes* (Alloptidae), *Scutomegninia* (Avenzoariidae) and *Metingrassia* (Xolalgidae). We found 110 adult male *M. neotropica* as well as hundreds of larvae, nymphs and adult females. We assessed only the position of adult males. Adult males were found on nine of the 16 cormorants examined. Of the 110 males, 91 were securely positioned in interbarb channels at the time of observation and 19 were loose on the feathers. 79% of the 110 males (n = 87) were homeomorphic, and 21% (n = 23) were heteromorphic. Exactly 50% of the males were left-handed (n = 55) and 50% were right-handed. There was no significant relationship between homeo- or heteromorphy and left- or right-handedness (homeo: 46 left, 41 right; hetero: 9 left, 14 right; Fisher's Exact Test 2-tailed P = .349).

Please cite this article in press as: Proctor, H., Knee, W., Asymmetry and polymorphism in males of the feather mite *Michaelia neotropica* Hernandes and Mironov (Acariformes: Astigmata: Freyanidae). Zool. Anz. (2018), https://doi.org/10.1016/j.jcz.2018.01.010