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Permanent female mimics in a lekking shorebird

Joop Jukema[1] **and Theunis Piersma**[2,3,*]

[1]*Haerdawei 62, 8854 AC Oosterbierum, The Netherlands*
[2]*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*
[3]*Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*
**Author for correspondence* (*theunis@nioz.nl*).

Female mimics are known from many species, but permanent, non-conditional, alternative mating strategies are only known from an isopod, a fish, a lizard and a bird. The single bird example refers to lek-breeding ruffs *Philomachus pugnax*, a shorebird for which two strategies (independent and satellite) have been known for over 50 years. Ruffs also provided the single case of an animal with two, rather than three, permanent alternative mating strategies. Here, we describe a rare female-like morph of ruffs: the 'missing' third alternative mating strategy, which we have called 'faeder'. Faeders are slightly larger than females and in late April have testes 2.5 time the size of testes of normal males. On leks in aviaries and in the wild they appear to combine feminine and masculine behaviours. Faeders may represent the ancestral, care-giving, male strategy, but their relatively large testes suggest that currently they behave as sneakers.

Keywords: alternative mating strategies; alternative phenotypes; mimicry; *Philomachus pugnax*; plumage variation; sexual size dimorphism

1. INTRODUCTION

In the fierce competition for mates and space, it sometimes pays for males to disguise themselves as females (Andersson 1994; Gross 1996). Female mimics are known from various arthropods, a mollusc, and from several groups of vertebrates, especially fish (Andersson 1994; Wikelski *et al.* 1996; Shine *et al.* 2001; Sinervo 2001; Hall & Hanlon 2002; Shine 2003; Goncalves *et al.* 2005), but they usually represent conditional, non-genetic, strategies (Gross 1996). Among many species of birds, males look like females when they are immature (Saetre & Slagsvold 1996), but no examples exist of males permanently mimicking female body size and plumage. Here, we describe a surprising new and rare, female-like morph among ruffs *Philomachus pugnax* that seems to represent a third permanent alternative mating strategy.

Ruffs are highly sexually dimorphic lekking sandpipers of a subfamily (Calidrinae, family Scolopacidae) that is notorious for its wide variety of mating systems (Pitelka *et al.* 1974; Myers *et al.* 1982; Piersma *et al.* 1996). Ruffs provide the only example among birds of genetically determined alternative reproductive strategies (Hogan-Warburg 1966; van Rhijn 1973, 1991; Lank *et al.* 1995). This dichotomy includes an 'independent' strategy of males that attempt to defend small mating courts against other independents on a lek and a 'satellite' strategy of males tolerated on leks by independents and stealing copulations with visiting hens when independents are temporarily distracted (van Rhijn 1973, 1990; Lank *et al.* 1995; Hogan-Warburg 1966; Widemo 1998). The two alternative mating strategies: (i) are strongly correlated with the coloration of the breeding plumage, (ii) show a slight difference in body size, (iii) are maintained for life and (iv) are consistent with a single-locus, two-allele autosomal genetic polymorphism (Lank *et al.* 1995; Bachman & Widemo 1999). The evolution of these alternative mating strategies and the maintenance of their relative frequencies (5–15% of male ruffs are satellites) appear to reflect female choice (van Rhijn 1983; Hugie & Lank 1997; Widemo 1998).

2. MATERIAL AND METHODS

Since the early 1980s, in the west of the province of Friesland every spring many tens to a few thousand ruffs are captured with a traditional netting method, the 'wilsternet' originally designed to catch Eurasian golden plover *Pluvialis apricaria* (Jukema *et al.* 2001; Piersma & Jukema 2002). The birds are ringed, weighed to the nearest gram, and their wing length measured to the nearest millimetre. Ruffs are the most sexually dimorphic sandpiper (e.g. Piersma *et al.* 1996), but sometimes intermediate sized birds were encountered and some of these were collected for inspection (see Jukema & Piersma 2004). In spring 2004, 1134 ruffs were colour-ringed using individual combinations of four colour-rings and one 'flag' (see figure 1*a*). The morphometrics of these birds was collected as well, as was a small 30 µl blood sample from the wing vein, stored in 98% ethanol. This sample included nine birds intermediate in size between males and females (with wing length between 170 and 180 mm). A total of 22 birds with intermediate sizes have now been molecularly sexed using the standard assays verified for another sandpiper (red knot *Calidris canutus*; Baker *et al.* 1999) and now also for ruff (Jukema & Piersma 2004).

From early April to late June 2004, we kept 22 ruffs together in an aviary 40×10 m and 4 m high at the Royal Netherlands Institute for Sea Research on Texel, The Netherlands. The group included five intermediate sized birds (subsequently confirmed to be males by molecular sexing in two cases, by dissection in the remaining three), six independent and four satellite males and seven females, all individually identifiable by plumage and colour-rings (see figure1*b*). From 14 May to 11 June, we observed these birds daily for *ca* 8 h. Observation effort was distributed over the period between 7 and 21 h in four blocks of two hours. Between 11 and 23 June, observations were more infrequent. We tallied all the copulatory attempts and recorded the identity of the individuals participating in the acts.

3. RESULTS AND DISCUSSION

In our catches, we encountered small numbers of female-plumaged birds (figure 1*a*) that were intermediate in size between females and males (figure 2*a*) and in spring developed a female-like feather type (figure 2*b*). These striped feathers possibly represent the original alternate plumage of sandpipers, rather than being homologous to the showy feathers of the supplemental plumage additionally developed by males (Jukema & Piersma 2000). Nevertheless, in all 22 cases where blood samples were collected, 'intermediate' birds were molecularly identified as males. In an overlapping sample of 18 such birds, sex was additionally confirmed by the presence of testes. During a period when we had good samples for both normal and small-sized female-plumaged males, the

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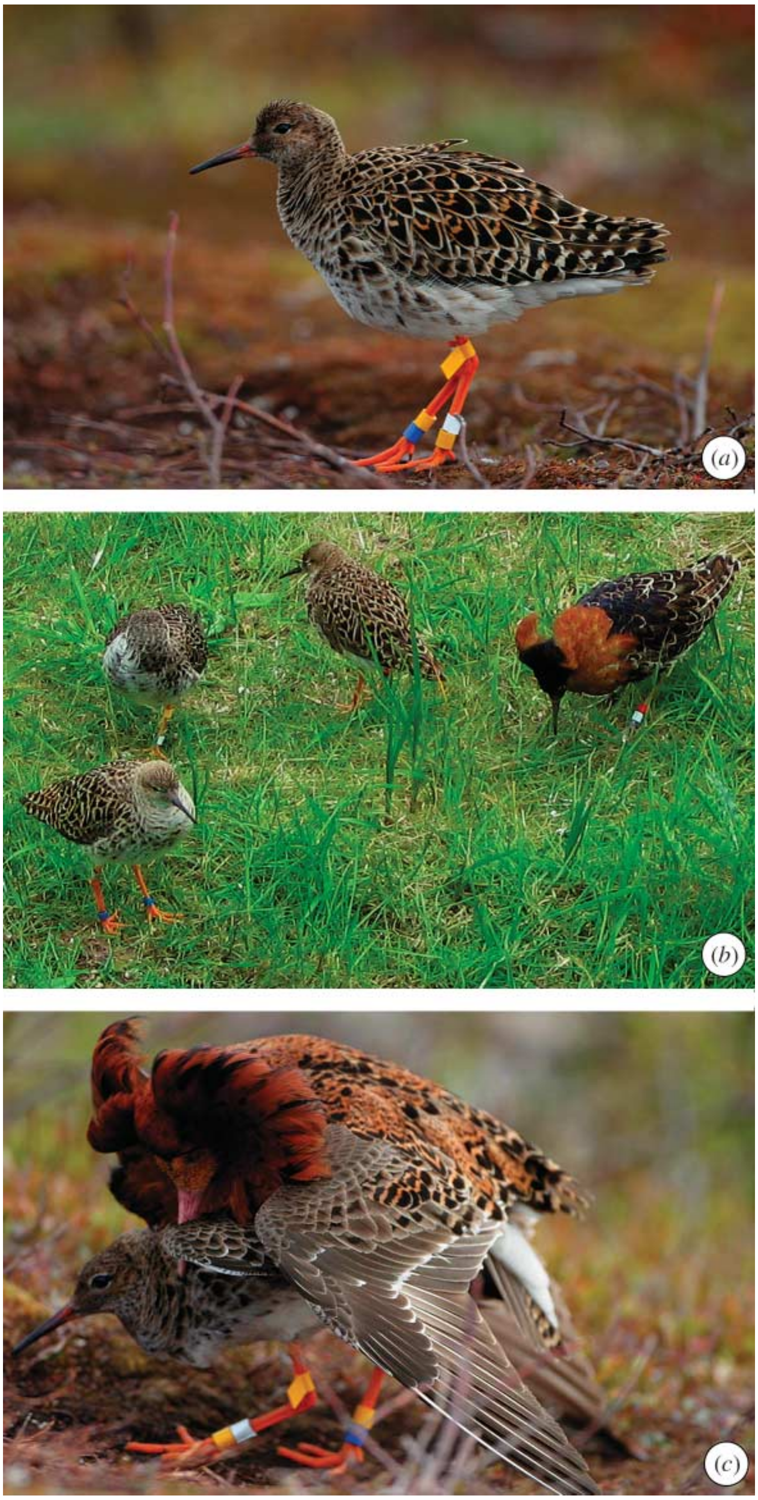

Figure 1. (*a*) A female mimic (or faeder), individually colour-ringed in The Netherlands on 10 April 2004, photographed while visiting a lek in Varanger, northern Norway, from 16 to 19 June 2004 (photo by J. and T. Champion). (*b*) On the left two female mimics, on the right an independent male and between them a single female in an aviary setting (photo by Y. Verkuil). (*c*) The individually colour-ringed female mimic is mounted by an independent male on a lek in Varanger, northern Norway, on 17 June 2004 (photo by J. and T. Champion).

testes of intermediate female-like birds were 2.5 times larger in volume than in normal males (average total testes volumes of 715 and 283 mm^3 in 5 female mimics and 15 normal males, respectively, caught in the period 10–25 April; pooled variance $t=-3.6$, $p=0.002$). Female mimics were aged as second year birds and older; when held for 2 years in captivity they showed no change. We have proposed to call this permanent and rare morph (1% or fewer of the birds in any 1 year) the ‘faeder’, an Old-English word for father (Jukema & Piersma 2004).

In the aviary study, from 14 May to 23 June 2004, we witnessed 25 copulatory attempts involving faeders, in 13 of which faeders were mounted by independent males (including the single case with clear cloacal contact). In seven cases, a faeder mounted an independent male, in four cases a satellite and once a female was mounted. Females never mounted males.

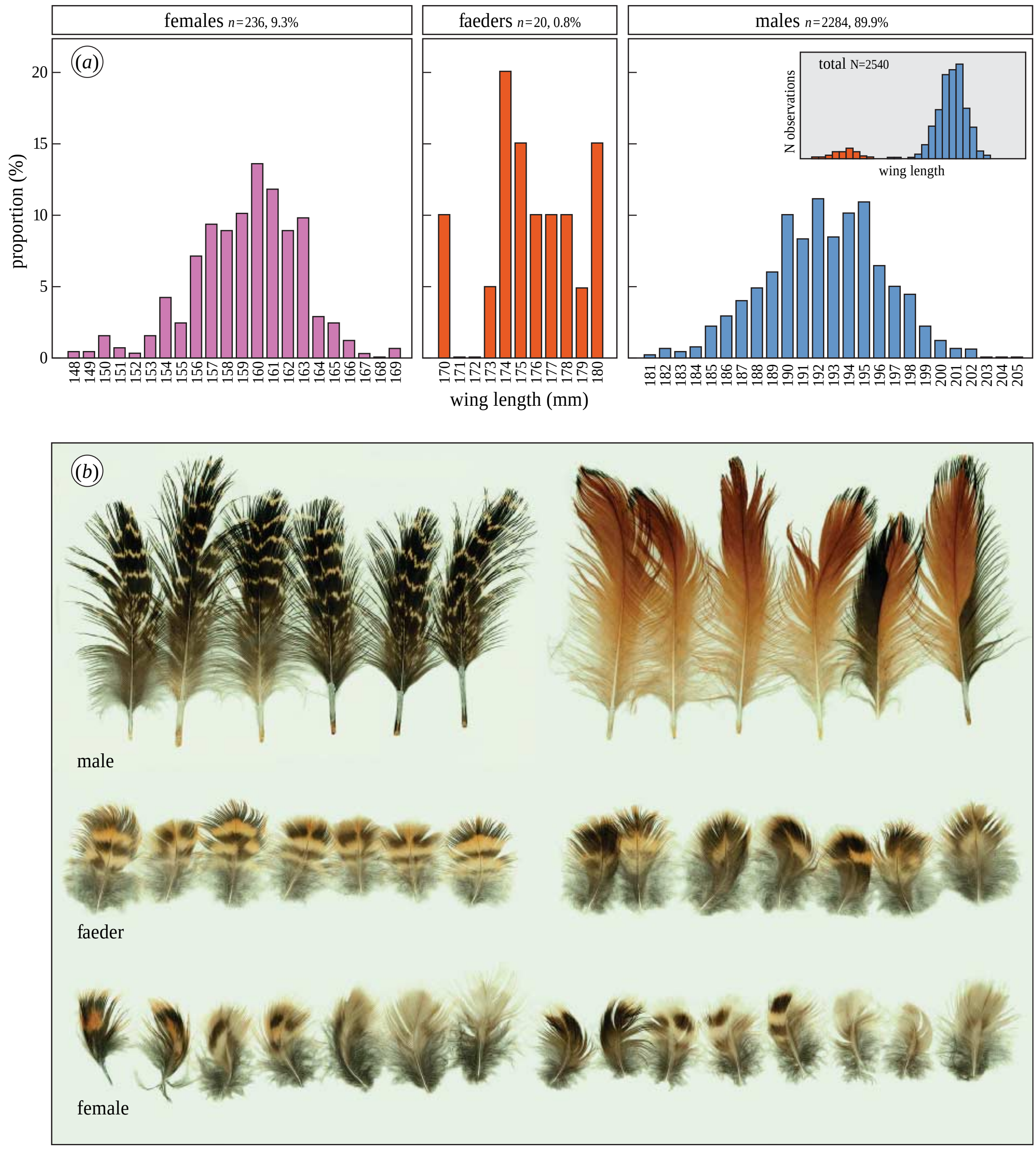

Figure 2. (*a*) Relative frequency distribution of wing lengths of the three categories of ruffs captured during northward migration in the northern Netherlands (2001–2004). Of the 20 birds with wing lengths between 170 and 180 mm, 11 were bled and in all cases they were molecularly confirmed to be males; the sex of 25 additional females and 28 males was also molecularly confirmed. (*b*) Samples of breast feathers of the nuptial plumage of two typical males (top), two female mimics or ‘faeders’ (middle row) and two females (bottom) of ruffs staging in April in The Netherlands. In female mimics and females these feathers represent the original alternate plumage, in males an additional, supplementary plumage (Jukema & Piersma 2000).

The feminine behavioural ploys of female mimics were confirmed in the field, with observations in northern Norway of an individually colour-banded faeder (molecularly sexed as male; figure 1*a*,*c*). This bird visited a lek from 16 to 19 June 2004, and was mounted by an independent male on 17 June and by a satellite on 19 June (figure 1*c*; J. Champion and T. Champion 2005, personal communication).

That faeders were as often ‘on top’ in homosexual mountings as ‘true’ males, suggests that their identity is known by the other males; they may appear to be ‘female mimics’ to us, but not necessarily to the ruffs themselves. The present observations may explain the rare ‘female–female’ mountings seen by dedicated ruff observers in the past (J. G. van Rhijn & J. Brinkkemper 2004, personal communication). As envisioned by van Rhijn (1985), faeders may represent the ancestral male type, but their relatively large testes suggest that currently they behave as sneakers (Taborsky 1994). Interestingly, the only other documented cases of permanent alternative strategies, in an isopod (Shuster & Wade 1991), a fish (Ryan *et al.* 1992) and probably a lizard (Sinervo & Lively 1996), also include three morphs, both representing three alleles at a single locus (Gross 1996). Do faeders similarly reflect the presence of a novel third allele, maintained in the population by negative frequency dependent selection? Or do faeders represent the expected 1% of ruffs homozygous for the satellite allele (Lank *et al.* 1995), a feature undisclosed in the single captive breeding study so far?

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