Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds

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A survey of 166 hummingbird species reveals novel associations of bill-length sexual dimorphism (BLSD) with plumage and breeding behaviours. Across all species, female bills become proportionately longer than male bills (higher female-to-male BLSD ratio) as sexual dichromatism increases. However, male bills are proportionately longer (lower female-to-male BLSD ratio) in both lekkeepers (traditional group display) and clustered breeders (female harems or colonial nests) compared with dispersed breeders. The overall positive association of plumage with BLSD suggests that social status determines priority of access to nectar-providing flowers. Furthermore, the distinctive BLSD associated with breeding aggregations may arise from behaviours that impose constraints on the usual male priority at flowers: female dominance over males around nest colonies and male residence on lek-mating territories. These various factors appear to alter plumage and bill characters of both sexes to produce the range of dimorphisms within the various dispersed and aggregated breeding system categories. Feedback loops caused by ecological consequences of breeding behaviour may alter the evolutionary dynamics of breeding systems, bird–plant interactions, and competing pollinators, as well as help explain the lek paradox.

Keywords: coevolution; lek paradox; natural selection; plumage coloration; sex roles; sexual selection

1. INTRODUCTION

Ecological studies of hummingbirds suggest that various forms of sexual dimorphism have interrelated causes. Hummingbirds (Trochilidae) have evolved sexual dimorphism in many of their characteristic attributes, including plumage coloration, bill morphology and foraging strategy. A strong case can be made that the hummingbird bill is a paradigm of ecological adaptation, as both experimental and observational studies suggest that characteristics of the bill are directly related to flower feeding (Feinsinger & Colwell 1978; Paton & Collins 1989; Temeles 1996; Temeles & Roberts 1993). However, hummingbird foraging behaviours are also strongly tied to reproductive behaviours because competitors and floral densities determine if males hold nectar-centred breeding territories or adopt alternative mating strategies (Pitelka 1942; Stiles & Wolf 1979; Payne 1984). Studies of particular species also suggest that foraging behaviours link plumage and bill-length sexual dimorphism (BLSD). Thus, aggressive feeding strategies are associated with bright iridescent plumage either in males of dichromatic species or in both sexes of monochromatic species (Wolf 1969; Bleiweiss 1985, 1992a,b, 1997). Moreover, bright sexually monochromatic plumage and sexual codominance at shared nectar sources often are paralleled by reduced sexual dimorphism in bill length (Wolf 1969; Bleiweiss 1985, 1992b). Therefore, the potential for interaction and feedback among different sources of selection (foraging behaviours, sex roles and sexual selection) or their many potential targets (plumage, bill length, breeding behaviour) is obvious.

Herein I test two hypotheses that follow from the evidence that both feeding and breeding biology affect sexual dimorphism in hummingbirds: first, that plumage and BLSD (here defined as the female-to-male ratio) are positively associated across the family; and second, that breeding systems affect the bill–plumage interrelationship. Support for both patterns suggests that foraging behaviours link plumage and BLSD to patterns of social dominance for non-sexual resources, and that breeding systems constrain dominance patterns if males gather at traditional breeding sites (leks) or if females form breeding aggregations (nest colony and/or harem). These more complex ecological dynamics better describe the origins of sexual dimorphism and provide new insights into otherwise problematic phenomena such as the paradoxical choosiness of females on leks (Darwin 1871; Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991; Höglund & Alatalo 1995).

2. MATERIAL AND METHODS

My survey includes roughly half of all hummingbird species from each of the two basal sister groups in the family, the hermits (Phaethornithinae) and non-hermits (Trochilinae). Numerous representatives from each of the principal lineages within each subfamily (Bleiweiss *et al.* 1994, 1997) are included. Thus, the sample of taxa should be representative of overall patterns in the family.

(a) Morphology

Data on bill lengths and plumage were obtained for 166 species from museum specimens (R. Bleiweiss, personal data) or from the literature (primarily Ridgway 1911; Wetmore 1968; Hinkelmann 1996). The standard measure of exposed culmen

was used to assess bill length, except that Wetmore (1968) reported culmen length as measured from the base. To minimize the effects of different estimates of bill length, I used the values for each sex from each source to calculate sexual dimorphism (from means for each sex) prior to combining values for overall species means. The highly significant correlation between measurements for taxa in both museum and literature data ($p < 0.001$) suggests that the quality of information from different sources is comparable and that these data can reasonably be combined. Sexual dimorphism in bill length was calculated as the ratio of mean female to mean male bill length (> 1 in most hummingbird species; Paton & Collins 1989). I also obtained data on body-mass sexual dimorphism for 106 of these same species to examine body-mass effects on BLS.

Plumage characteristics were quantified using indices developed earlier (Bleiweiss 1997). Briefly, the body was divided into 25 standard patches, which served as the basis for estimating both sexual dichromatism (integer scale from 0 for low dichromatism and 25 for high dichromatism) and plumage colourfulness and conspicuousness (COCO, integer scale from 0 for low to 50 for high values; see Bleiweiss 1997). Sexual dichromatism was estimated by summing the number of patches for which the sexes of each species differed in colour. Plumage COCO was estimated by summing the COCO scores of each patch for each sex: 0 if neither colourful nor conspicuous, 1 if either colourful or conspicuous, and 2 if both colourful and conspicuous (by the scheme devised in Bleiweiss (1997)). For both mensural and plumage characters, I broke data down by subspecies and then calculated and analysed species means.

(b) *Breeding behaviours*

Hummingbirds appear to express only polygynous breeding systems, and females conduct all duties associated with nesting and rearing of the young; the few reports of male parental care are atypical for those species and in any case remain unconfirmed (Johnsgard 1997). I focused on differences in breeding behaviours that impart either aggregated or dispersed spatial distributions, which define four broad aggregation categories based on the occurrence of male (lek) and/or female (nest colony and/or harem) aggregations: dispersed-nesting non-lekkers, dispersed-nesting lekkers, colony-harem breeding non-lekkers, colony-harem breeding lekkers (figure 1).

All known and suspected lekking taxa (compilations in: Atwood *et al.* 1990; Johnsgard 1994, 1997; Bleiweiss 1997) were classified as lekkers (see Bleiweiss (1997) for criteria). Data are inadequate to distinguish classical dense lekkers, in which males are within visual range, from exploded lekkers, in which males are in only acoustical contact. However, species differ in their constancy of lekking, which is always expressed in some, but may be highly variable across regions or years in others (Stiles & Wolf 1979; Höglund & Alatalo 1995). As the frequency with which lekking is expressed may alter the consistency and magnitude of selection pressures associated with this mating system, I also distinguished 'fixed' from 'facultative' lekkers (figure 1). Colonial nesting is not well documented in hummingbirds but available data suggest that it occurs in the lekking genus *Topaza* (Nicholson 1931), and among non-lekkers in *Oreotrochilus* (Carpenter 1976) and probably in the *anaeocauda* superspecies in *Metallura* (Moore 1934, 1940; Fjeldså & Krabbe 1990). Females may also cluster during breeding if they form 'harems' (here used to indicate a group of females associated with a male) that conduct essential reproductive (nesting (*Glaucis*) or feeding (*Pantherpe*)) activities on the territory of the male with whom they

		male	
		dispersed (various)	aggregated (lek)
female	dispersed (various)	♂ non-lek	♂ lek
		♀ dispersed	♀ dispersed
	aggregated (colony-harem)	♂ non-lek	♂ lek
		♀ colony-harem	♀ colony-harem

Figure 1. Schematic representation of breeding system factors based on aggregation by one or both sexes. Panels indicate aggregated breeding behaviours of males (lek) and females (nest colony and/or harem). Thus, patterns of dispersion for males and females express four combinations in which one or the other or both sexes form aggregations during the breeding season.

are assumed to have mated (Wolf & Stiles 1970; Snow 1973). All remaining species were classified simply as dispersed polygynous breeders, which should serve to minimize differences between breeding categories because some outliers may eventually be found to be aggregated breeders.

(c) *Analyses*

To account for similarities caused by common descent, data were analysed with the phylogeny-based statistical method of independent contrasts (Felsenstein 1985; Garland *et al.* 1992, 1993). I constructed general linear models in which mating (lek versus non-lek) and nesting (colonial and harem versus dispersed) systems were coded as 1–0 categorical factors, and in which ordinal or continuous variables (dichromatism, COCO, body-mass sexual dimorphism, sex-specific body mass or bill length) were specified as covariates (analogous to a two-way ANCOVA; see figure 1). Models distinguished combinations of facultative or fixed lekkers (distinct or lumped), but lumped colonial and harem breeders (results for analyses that excluded harem breeders were qualitatively similar). Coefficients of the cross-product terms (analogous to interaction in ANCOVA and defined as the product of the standardized independent contrasts of two factors or a factor and covariate (Garland *et al.* 1993)) were used to test for significant differences in the slopes of regressions on contrasts. Significance levels are reported as two-tailed probabilities except for the directional hypothesis of BLS on sexual dichromatism (positive).

Independent contrasts were generated in the Phenotypic Diversity Analysis Program (Garland *et al.* 1993, 1999) and then imported into a standard statistical package (SAS for UNIX®) where contrasts were standardized (Garland *et al.* 1993) prior to analysis. Non-significant interaction terms were eliminated from consideration, and all regressions on contrasts were forced through the origin (Garland *et al.* 1993). Morphometric data were log₁₀-transformed prior to all analyses, with all ratios expressed as the difference in logs.

The phylogeny used for analysis of contrasts was constructed from phylogenies available in the literature, with preference given to trees estimated from molecular data (e.g. Gerwin &

Table 1. Significance of *t*-values for parameters in general linear models with BLSD (female–male) as a function of plumage (sexual dichromatism or male COCO) as covariate and mating (lek versus non-lek males) and breeding (colonial and harem versus dispersed females) aggregation as categorical factors

(Models differ in how breeding aggregations are classified (see text for descriptions of each category).)

independent variables ^{a,b}	plumage variable	
	dichromatism	male COCO
A (plumage)	1.840*	0.669
B (fixed lekkers versus others)	–2.100*	–0.743
C (colonial and harem versus others)	–3.864***	–2.972**
A × B	—	2.641**
A × C	—	0.113
B × C	—	1.185
A (plumage)	1.656*	–0.148
B (all lekkers versus others)	–1.845#	–0.658
C (colonial and harem versus others)	–3.958***	–2.616**
A × B	—	3.859***
A × C	—	1.784#
B × C	—	–0.111

^aIndependent contrasts were used to correct for phylogenetic effects on statistical significance.

^b*n* = 166, d.f. = 150 after taking polytomies into account.

p < 0.10, * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

Zink 1989, 1998; Gill & Gerwin 1989; Sibley & Ahlquist 1990; Bleiweiss *et al.* 1994, 1997). Branch lengths were not available for most regions of the tree, and were specified under a speciation model that set all branch lengths equal to 1. A gradual model in which characters experience more change along longer branches (Grafen 1989) was deemed unsuitable because this method did not standardize contrasts nearly as well as did an assumption of speciation change (Garland *et al.* 1992), and because the empirically determined tempo of hummingbird evolution appears to conform more to the speciation model (rate variation–non-contemporaneous tips; periods of rapid cladogenesis; Bleiweiss 1998). Polytomies and corresponding degrees of freedom for analyses of independent contrasts were handled as described in Purvis & Garland (1993).

3. RESULTS

(a) Dichromatism as a covariate

The fit of nested models with and without all higher-order (interaction) effects were not significantly different, so models without interaction were deemed suitable for these data. The reduced models indicate that male and female breeding aggregations have significant negative effects on an overall significant positive regression of BLSD on sexual dichromatism (table 1 and figure 2). Together, these results imply that male bills on average are longer (relative to female bills) for lekkers and colony–harem breeders across all levels of sexual dichromatism. As part of the overall lower mean BLSDs in hummingbirds with these breeding systems, the males of many species at the lower end of the dichromatism scale

Figure 2. Scatter plots of raw species values of BLSD as a function of sexual dichromatism and male COCO. Symbols identify breeding aggregation category, and symbol size is proportional to the number of taxa with that combination of values.

often have bills longer than those of females (BLSD < 1), the opposite of the usual pattern in hummingbirds (figure 2). The taxon that combines both forms of breeding aggregation, *Topaza*, occupies the highest end of the dichromatism scale but has anomalous BLSD < 1 as well. In terms of the general linear model, the unique combination of characters in *Topaza* can be understood as a consequence of additive effects of both female (colonial nesting) and male (lekking) breeding aggregation. Facultative lekking appears to weaken these associations somewhat, as mating system effects were smaller (*p* < 0.10) in models that lumped fixed and facultative lekkers.

(b) Male COCO as a covariate

Interpretation of individual effects in models with male COCO as covariate is complicated by evidence of significant interaction, particularly for male COCO and lek versus non-lek breeding system (table 1, figures 2 and 3), a pattern that is general among birds (Bleiweiss 1997). Specifically, the plumages of lekkers define a graded series from dull monochromatic to bright dichromatic, whereas the plumages of non-lekkers are more varied and include brighter monochromatic and duller dichromatic species (figure 3). Thus, sexual plumage differences and male COCO track each other closely only in lekkers (figures 2

Figure 3. Scatter plots of raw species values of male COCO as a function of sexual dichromatism. Symbols identify breeding aggregation category, and symbol size is proportional to the number of taxa with that combination of values.

Table 2. Significance of *t*-values for parameters in general linear models with BLSD (female–male) as a function of plumage sexual dichromatism and body-mass sexual dimorphism as covariates and mating (lek versus non-lek males) and breeding (colonial and harem versus dispersed females) aggregation as categorical factors

(Models differ in how mating aggregations are classified (see text for descriptions of each category).)

independent variables ^{a,b}	fixed lekters	all lekters
A (sexual dichromatism)	3.161**	2.944**
B (lekters versus others)	–2.527*	–1.465
C (colonial and harem versus others)	–0.922	–0.936
D (body-mass sexual dimorphism)	1.281	1.410

^aIndependent contrasts were used to correct for phylogenetic effects on statistical significance.

^b*n* = 106, d.f. = 100 after taking polytomies into account.

p* < 0.05, *p* < 0.01.

and 3). As part of the general positive association among lekters between BLSD and male COCO, a high proportion of dull monochromatic lekters have BLSDs < 1 (figures 2 and 3).

(c) Contributions to sexual dimorphism by mass

When added to the general linear models, body-mass sexual dimorphism does not contribute significantly to BLSD (table 2). Thus, lower BLSD in lekters cannot be ascribed to significant differences in body-mass sexual dimorphism among the breeding system categories. A reduction in sample size for analyses that include body mass as covariate may account for non-significant effects of the female breeding system in some of these models, as species with female breeding aggregations are few even in the full data set (figure 2).

Table 3. Significance of *t*-values for parameters in general linear models testing male and female contributions to sexual dimorphism in plumage and bill length

(Plumage model: sexual dichromatism = male COCO + female COCO. Bill length model BLSD = mean male bill length + mean female bill length.)

sex ^{a,b}	dimorphism	
	plumage	bill length
male	13.144***	–826.644***
female	–10.431***	722.204***

^aIndependent contrasts were used to correct for phylogenetic effects on statistical significance.

^b*n* = 166, d.f. = 150 after taking polytomies into account.

****p* < 0.001.

Table 4. Significance of *t*-values for parameters in general linear models with BLSD (female–male) as a function of sex-specific bill length and body mass as covariates and mating (lek versus non-lek males) and breeding (colonial and harem versus dispersed females) aggregation as categorical factors

(Analyses were the same as previous models.)

independent variables ^{a,b}	males	females
A (sex-specific bill length)	–3.089**	–0.671
B (sex-specific body mass)	–0.237	–1.736#
C (fixed lekters versus others)	–3.346**	–3.085**
D (colonial and harem versus others)	–0.776	–0.613
A (sex-specific bill length)	–2.692**	–0.306
B (sex-specific body mass)	–0.121	–1.498
C (all lekters versus others)	–1.649	–1.655
D (colonial and harem versus others)	–0.827	–0.706

^aIndependent contrasts were used to correct for phylogenetic effects on statistical significance.

^b*n* = 106, d.f. = 100 after taking polytomies into account.

#*p* < 0.10, ***p* < 0.01.

(d) Contributions to sexual dimorphism by males and females

Male and female plumage colour (COCO) and bill length contribute to sexual dichromatism and BLSD, respectively (table 3). Notably, contributions by sex-specific bill length to BLSD are greater for males than for females, even when controlling for the effects of sex-specific body mass (tables 3 and 4). A highly significant negative association between sexual dichromatism and sex-specific bill length based on analysis of standardized independent contrasts (males: *t* = –3.617, *p* < 0.001; females: *t* = –3.265, *p* < 0.01) indicates that the bills of both sexes are shorter on average in more dichromatic species.

4. DISCUSSION

My analysis of hummingbirds indicates that BLSD covaries with plumage, and that mating and nesting aggregations have significant mean effects on the

bill–plumage interrelationship. Moreover, consideration of plumage and breeding system as independent variables also implies that social behaviours may determine ecomorphology (BLSD as dependent variable), not just vice versa (Emlen & Oring 1977). Herein I develop a general evolutionary framework connecting the various forms and causes of sexual dimorphism. I first address the implications of covariation between bill and plumage characters and then examine breeding system effects under these considerations.

(a) *Foraging behaviour and the evolution of sexual dimorphism*

In sexually dimorphic hummingbirds, the shorter bills and brighter plumages of the males are associated with their dominance over females, who are forced to feed at more dispersed nectar sources (Wolf 1969; Paton & Colins 1989; Temeles 1996). The fundamental question, therefore, is whether bill and plumage dimorphisms are complementary adaptations for sexual differences in foraging strategy. With respect to bill dimorphism, functional analyses indicate that sexual differences in bill length have important consequences for foraging efficiency. The shorter male bill appears to reduce handling time at shorter corolla flowers they typically defend, which is advantageous for the overall time-minimizing strategy employed by aggressive territorial birds (Temeles 1996). By contrast, the longer bill in socially subordinate females improves their exploitation abilities at longer corolla flowers in several related ways, including more efficient extraction rates from longer flowers, the ability to discourage visitation by shorter-billed hummingbirds through nectar depletion, and increasing the depth at which nectar left over by shorter-billed species can be reached. Thus, empirical data support the hypothesis that sexual differences in bill length are closely associated with the different behavioural strategies of nectar exploitation by male and female hummingbirds.

Considerable evidence has now been adduced that plumage coloration in hummingbirds relates to intersexual and interspecific social interactions in competition for nectar, with brighter plumage in the more dominant species, sex, or morph (Pitelka 1942; Wolf 1969; Bleiweiss 1985, 1992a,b, 1997). This hypothesis is strengthened further by my results linking plumage with foraging behaviour through the significant relationship between plumage coloration and bill morphology. Indeed, this interspecific pattern parallels intersexual patterns in plumage, dominance and bill dimorphism in three respects. First, BLSD increases with sexual dichromatism. Thus, the intersexual difference in bill length appears to depend on differences in dichromatism and hence, on male aggression. Second, the bills of more dichromatic species are shorter than those of less dichromatic species, suggesting that selection for shorter bills operates more strongly in more dichromatic and hence, more aggressive, species. Third, both sexes contribute to patterns of sexual dichromatism, implying that selection associated with the distinct behavioural strategies of each sex influence sexual differences in plumage; by contrast, sexual selection should affect primarily males in polygynous species (see also Bleiweiss 1992a,b). In the context of the functional basis for intraspecific patterns of bill and plumage

Figure 4. Schematic diagram for possible evolutionary responses of BLSD to social status (indicated by plumage) and breeding system. Lower sexual dichromatism (x -axis) indicates lower social status and greater effects of intraspecific competition (between the sexes). The 1 on the y -axis marks sexual monomorphism in bill length. Possible outcomes include selection for a single optimal bill dimorphism suited to each breeding system (lower dashed line), or selection for a graded series of bill dimorphisms (upper dashed or solid lines) as a function of social status (as indicated by plumage coloration).

dimorphism, these considerations suggest that the same ecological factors operate broadly across hummingbird species.

The hypothesis that plumage and BLSD evolve through intersexual divergence in foraging ecology is strengthened further by evidence that bill lengths are more similar in the sexes of monochromatic species (Wolf 1969), a pattern amplified by my results. However, foraging behaviour alone does not account for the evolution of longer bills in males of some (typically dull monochromatic) species. This additional effect arises from more general breeding system effects layered over the plumage–bill covariance. Based on the hypothesis that plumage indicates social status in relation to feeding strategy, however, breeding system effects on bill length and BLSD appear to depend on social dominance as indicated by colour. Thus, a range rather than a single (optimum) phenotype characterizes each breeding aggregation category (figure 4). The most obvious consequence of social dominance is to determine priority at limiting resources. Thus, breeding system effects on BLSD may arise from deviations in the usual priority of each sex at flowers and how much these relationships are influenced by social status (plumage).

(b) *Breeding system effects on dimorphism*

Available natural history data provide a strong basis for understanding why male bill length changes in conjunction with different breeding systems. *Oreotrochilus estella* is a non-lekking colonial nester with longer bills in males than in females. Detailed studies of this species suggest that the probable source of selection for altered BLSD is in fact priority at limiting resources. Breeding female *O. estella* express resource-centred territoriality, defending gorges that provide nest sites and the richest feeding areas

(Carpenter 1976). Males occasionally visit female territories to display, but otherwise female dominance restricts males to the more dispersed nectar sources outside the gorges, where territoriality is difficult (Carpenter 1976). Outside the breeding season the sexes' foraging and other behaviours are similar to each others'. Thus, the unusual bill dimorphism in *O. estella* coincides with unusual female dominance behaviours that enforce spatial separation of the sexes and limit male access to floral resources.

Spatial separation of the two sexes also occurs in lekking birds because males compete for communal display territories that they occupy for long periods during the day and year whereas females visit leks only briefly (Stiles & Wolf 1979; Atwood *et al.* 1990; Höglund & Alatalo 1995). Although overt intersexual aggression does not appear to determine where male leks occur, male attendance at the lek implies that their priority at nectar sources is reduced; males must forage away from the lek (by definition; see Stiles & Wolf (1979) for details on this pattern for hermits) in an environment whose resources may be depleted by birds unencumbered by the need to attend a lek, including female conspecifics and individuals of other species. Such a general constraint may select for longer bills in lekking males to improve their abilities as exploitation competitors (by the same mechanisms outlined above for the case when females are the subordinate sex). The range of intersexual bill-length ratios may then arise from the different ways male priority is affected by social status (plumage). Thus, brightly coloured males of interspecifically dominant lekking males can physically displace some species and may evolve longer bills (lowering the female-to-male ratio) that mitigate interspecific exploitation competition. The competitive environment experienced by dominants does not mandate, however, that male bills are longer than those of conspecific females. By contrast, both sexes of socially subordinate lekking birds such as hermits are limited to those resources not controlled by dominants, and potential competition appears to be mainly intraspecific (for details, see Stiles & Wolf 1979). Thus, lekking males of subordinate species are more likely to be under selection to reduce intraspecific exploitation competition with females; under these circumstances, males may be selected to evolve bills that are longer than those of female conspecifics.

These considerations predict that spatial segregation of the sexes caused by the combination of male lekking and female coloniality would doubly compromise male priority, whereas breeding aggregations that lack separation of the sexes (harem polygyny) would not. As demonstrated herein, the combination of male (lek) and female (colonial nesting) aggregations in *Topaza* accompanies (apparently) additive effects on BLSD (taking account of plumage as covariate). Remarkably, female *Topaza* also are territorial around the nest and codominant with males at more distant feeding sites during the breeding season (Nicholson 1931). These behaviours parallel the female dominance observed in non-lekking birds that nest colonially (*Oreotrochilus*). Thus, intraspecific social relations in *Topaza* appear to generate both of the constraints on male priority at flowers, lekking and female aggression, expressed separately if at all in other hummingbirds. Conversely, the sexes are codominant and exploit the

same patch of flowers in hummingbirds with harem polygyny (*Glaucis*, *Panterpe*), which express subequal bill lengths (nearly 1:1 in both genera).

The priority hypothesis presented herein appears to account for a host of phenomena that would otherwise be puzzling. Reduced male priority at flowers in species with male (lekking) or female (colonial nesting) aggregation provides a mechanism whereby males can evolve trophic features analogous to those of the longer-billed females in dichromatic non-lekking species with brightly coloured and aggressive males. Under this hypothesis, species with plumages as different as hermits (dull monochromatic) and *Topaza* (bright dichromatic) can evolve the same unusual bill dimorphism ($BLSD < 1$) through analogous social dominance constraints: interspecific subordination coupled with lekking in hermits, intraspecific subordination coupled with lekking in *Topaza*. Indeed, dominance behaviours by female *Topaza* may have selected for the unusually bright female plumage (iridescent golden green with a red throat patch) in this dichromatic species. Although I failed to detect interaction between male and female breeding systems, most colonial nesters have $BLSD < 1$, whereas lekking birds adhere more closely to the general covariation of BLSD with sexual dichromatism (figures 2 and 4). Analysis of a larger sample of colonial nesters will be required to determine if mating and nesting behaviours impart different covariance patterns of dimorphism (figure 4).

(c) *Implications for evolutionary dynamics*

The integration of feeding and breeding behaviours may influence the dynamics of coadaptation between the sexes or species in various contexts. For example, the association of mating systems with patterns of trophic dimorphism suggests that reproductive behaviours are linked to coevolution between organisms and the resources they exploit (e. g. hummingbirds and their flowers). Moreover, the strong ecological selection pressures on lekking birds implied by several patterns reported herein and elsewhere (Bleiweiss 1997; Westcott 1997) provide an orthodox mechanism for maintaining genetic variation among males with such mating behaviour. Ecological feedback on lekking males may help explain the lek 'paradox' (Kirkpatrick & Ryan 1991) of why and how females maintain strong preferences in the absence of any apparent contribution by males to female fitness.

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