Behavioral Ecology
doi:10.1093/beheco/arh135
Advance Access publication 21 July 2004

Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps

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Elaborate secondary sexual traits, such as the ornamental plumage of birds, may be favored by female choice because they serve as honest indicators of male quality. Elaborate traits are thought to be honest signals because they are expensive to produce and increase predation risk. Here we investigate another potential cost of elaborate traits, i.e., the time and energy required to maintain them in good condition. We tested the hypothesis that species of birds with ornamental plumage invest more time in maintenance behavior than do related species without such plumage. To test the hypothesis we quantified the maintenance behavior of nine ornamental and nine non-ornamental species in aviaries and zoos. To test the validity of using captive birds, we first collected data on 12 captive species for which data from wild individuals were also available. The maintenance times of captive and wild individuals were highly correlated across species. Maintenance time was also correlated with plumage length, independent of body size. Ornamental species had longer plumage than non-ornamental species, and they devoted significantly more time to maintenance. Time spent on maintenance cannot be devoted to other activities. This temporal trade-off reinforces the honesty of ornamental plumage. We suggest that high maintenance handicaps are present in a variety of animals. *Key words:* comparative study, grooming, indicator mechanisms, sexual selection, time budgets. *[Behav Ecol]*

Elaborate secondary sexual traits, such as the proverbial peacock's tail, are assumed to provide females with honest information about male quality (Andersson, 1994). The indicator function of these traits is thought to be reinforced by the physiological costs associated with production of the traits. All other things being equal, ornamental traits may also make the bearer more vulnerable to predators. Yet another potential cost of ornamental traits is the time and energy needed to maintain them in good condition. Despite its intuitive appeal, we know of no study that has tested for such "high maintenance" handicaps. In this paper we report the results of such a test using birds. We tested the explicit prediction that species of birds with ornamental plumage devote more of their daily time-activity budgets to maintenance behavior than do related species with less elaborate plumage.

Birds, mammals, and insects spend considerable time engaged in maintenance behavior, such as grooming (Barber et al., 2000; Cotgreave and Clayton, 1994; Hart et al., 1992; Kovac, 1993; Murray, 1990; Tanaka and Takefushi, 1993). Birds keep their plumage in good condition using a variety of main and subsidiary maintenance behaviors, including preening, scratching, bathing, dusting, sunning, anting, shaking, and ruffling of the feathers (Moyer and Clayton, 2004; Moyer et al., in press; Simmons 1964, 1985, 1986). Across species, birds average 9.2% of their daily time budget on maintenance (Cotgreave and Clayton, 1994). Effective maintenance behavior has been shown to require a significant amount of energy (Croll and McLaren, 1993). Furthermore, the time and energy devoted to maintenance detracts from other behaviors, such as feeding and vigilance (Redpath, 1988). These trade-offs should reinforce the maintenance costs associated with ornamental traits, keeping them honest signals. In short, animals are expected to invest the least amount of time possible in maintenance, while keeping their ornamental traits in good enough condition to attract a mate.

Quantifying the maintenance behavior of wild animals is a challenge because it is difficult to observe most individuals for long, uninterrupted periods of time in most habitats. However, since the amount of time devoted to maintenance has a strong genetic basis (Greer and Capecchi, 2002), it is likely that the relative grooming rates of different wild species will be reflected in captive individuals of these same species, making it possible to test the high maintenance hypothesis using captives. We tested the feasibility of this approach by comparing the maintenance times of 12 species observed both in the wild and in captivity. We then used captive birds to compare the maintenance times of nine ornamental species and nine non-ornamental related taxa to test the hypothesis that ornamental species devote more time to maintenance behavior.

In addition to collecting behavioral data, we collected data on a variety of plumage and other morphological traits that might be correlated with maintenance behavior. For example, we examined components of bill and foot morphology that could influence grooming efficiency. Indirect evidence for the importance of bills and feet as grooming tools comes from two comparative studies. The first study showed that birds with long bills spend proportionally more time scratching with their feet than do birds with short bills, presumably as compensation for the unwieldiness of long bills (Clayton and Cotgreave, 1994). The second study suggested that birds with longer bill overhangs are more efficient preeners because the overhang helps birds create a shearing force that crushes ectoparasites (Clayton and Walther, 2001).

METHODS

Maintenance behavior: wild/captive comparisons

The wild/captive data set contained 12 species. We used published data on wild birds for all of these species and published data on captive birds for two of the 12 species (see

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Received 30 March 2004; accepted 26 May 2004.

below). For the remaining 10 species, we collected original data from captives. Adult captive birds were observed in aviaries and zoos in England, Germany, and the USA (see Acknowledgements). The birds were housed in enclosures under semi-natural conditions with sufficient room for short flights. Captive species were observed for 10 h each. Individuals of each species were observed throughout the day (0900–1800 h) and for at least one h during each of the following intervals: 0900–1200, 1200–1500, and 1500–1800 h. After half an hour of observing one species, another species was observed, and so on, such that each species was observed over several days to even out effects of weather or other factors on particular days.

Maintenance time was defined as the mean percent of daylight hours a species devoted to maintenance behavior. Focal animal sampling was used to collect data on the behavior of captive birds (Altmann, 1974). If more than one bird was visible in the enclosure, the focal animal was chosen as follows. If individual birds could be distinguished reliably (by sex, plumage pattern, eye color, etc.), then observations were alternated among individuals. If individuals could not be distinguished, a random number between 1 and 50 was chosen. All individuals were then counted from the left to the right (several times if necessary) until the random number was reached; that individual was then observed.

Recording of behavioral data began as soon as the focal individual was spotted, and ended 30 min later, or when the individual disappeared from sight (which rarely happened). The duration of each maintenance behavior was recorded with a stopwatch that was started as soon as the behavior began and was stopped if more than 3 s elapsed without the behavior continuing (Clayton and Cotgreave, 1994). The time delay was necessary because birds habitually look up between bouts of maintenance behavior (especially preening), then quickly resume the behavior. The following behaviors were recorded: preening (including allopreening), scratching, stretching, head wiping, shaking and ruffling the feathers, bill and head rubbing, bathing, dusting and sunning (Simmons, 1964, 1985, 1986).

For each species of wild bird, published data were averaged across observation periods, then across sexes, and finally across studies when more than one published study was located per species. The species and data sources for wild birds were as follows: *Anas acuta* (Fasola and Canova, 1993; Migoya et al., 1994; Miller, 1985; Paulus, 1988 citing Hepp, 1982; Rave and Cordes, 1993; Roux et al., 1978; Rushforth Guinn and Batt, 1985; Tamisier, 1976; Thompson and Baldassarre, 1991), *Anas penelope* (Brunckhorst, 1996; Campredon, 1981), *Aythya fuligula* (Amat, 1984; Folk, 1971; Pedroli, 1982), *Colibri coruscans* (Schuchmann KL, personal communication), *Cygnus cygnus* (Black and Rees, 1984; Brazil, 1981), *Grus grus* (Alonso and Alonso, 1993), *Larus fuscus* (Delius, 1988), *Nyctea scandiaca* (Boxall and Lein, 1989), *Oxyura jamaicensis* (Bergan et al., 1989; Hughes, 1990; Johnsgard and Carbonell, 1996 citing Carbonell, 1983; Tome, 1991), *Phoenicopterus ruber* (Espino-Barros and Baldassarre, 1989a,b; Fasola and Canova, 1993), *Struthio camelus* (Williams et al., 1993), and *Threskiornis spinicollis* (McKilligan, 1979). Published captive bird data were also used for two species: *Larus fuscus* (Delius, 1988) and *Struthio camelus* (Deeming, 1998; McKeegan and Deeming, 1997).

Maintenance behavior: ornamental/non-ornamental comparisons

The 18 species for the ornamental/non-ornamental comparisons were all captive birds that were observed as described above, except that each of the species was observed for six h (except *Pavo cristatus*, which was observed for 30 h; see Walther, 2003). Nine of these species had obvious ornamental plumage traits; the other nine species did not have such traits (Table 1, Figure 1). Ornamental plumage was defined as any plumage whose functional purpose could not be explained by the requirements of flight or insulation. Ornamental plumage traits were located on different body parts, as follows: head (*P. cristatus*, *Geronticus eremita*, *Balearica regulorum*), neck (*Acryllium vulturinum*), wings (*S. camelus*, *Aix galericulata*), and tail (*Syrmaticus reevesii*, *P. cristatus*, *Gallus gallus*, *Urocissa erythrorhyncha*). The 18 species were categorized as ornamental or non-ornamental prior to any observations, and they represent a gradient of dimorphism; some species exhibit extreme dimorphism (e.g., *P. cristatus*) and some exhibit no dimorphism (e.g., *Cyanocorax mystacalis*). Only the ornament-carrying males were observed for the dimorphic species, while both males and females may have been observed for the monomorphic species. The data set was used to compare maintenance times of ornamental and non-ornamental species, as well as to test for possible morphological correlates of maintenance time.

Morphological variables

To test for an association between maintenance time and morphology, we collected morphological data for each of the 18 species in the ornamentation data set. With the exception of body mass (see below), morphological data were obtained as in earlier studies (Clayton and Walther, 2001; Walther et al., 1999) by averaging measurements from one male and one female specimen at the Natural History Museum, Tring, UK. Data were collected on the following traits:

- Body mass (g): data were taken from Bennett (1986), Dunning (1993), and Urban et al. (1986); data were averaged between sexes and then across published sources.
- Plumage length (mm): sum of the maximum length of feathers on six body regions (head, neck, back, breast, wing, and tail), including those where ornamentation occurs.
- Bill length (mm): distance between gape and most distal portion of the bill.
- Bill width (mm): horizontal distance between sides of the base of the upper mandible.
- Bill depth (mm): vertical distance between top of upper and bottom of lower mandible at deepest part of the bill.
- Bill overhang length (mm): length of overhang of upper mandible over lower mandible at the bill tip.
- Foot length (mm): distance from anterior end of tarsus to tip of nail on longest front toe.

Analyses

In comparative studies, it is important to consider the potential influence of phylogenetic relatedness of the species being compared on statistical results and deductive logic (Harvey and Pagel, 1991; Harvey and Rambaut, 1998; Nee et al., 1996; Read and Nee, 1995). In the case of the wild/captive comparisons, it was not necessary to control for phylogeny because we simply wanted to establish whether maintenance times of wild and captive birds are correlated. Thus, the question was not whether wild birds with higher maintenance times 'evolved' higher maintenance times in captivity. Rather, we simply asked whether differences in the maintenance times of captive birds could be used to extrapolate the behavior of wild birds.

In the second part of the study, however, it was necessary to control for the effects of phylogenetic relatedness of species because we asked whether differences in maintenance

Table 1

Maintenance times for ornamental and non-ornamental species and captive (C) and wild (W) individuals

		% Overall time in maintenance behavior		% Maintenance time budget spent on particular behaviors								
English name	Latin name	C	W	P	S	ST	WH	SR	R	B	D	SU
Greater Rhea[b]	*Rhea americana*	7.4	—	99.06	0.57	0	0.30	0.08	0	0	0	0
Ostrich[a]	*Struthio camelus*	3.7	1.4	97.47	0	2.53	0	0	0	0	0	0
Crested Guinea-Fowl[b]	*Guttera edouardi*	13.4	—	98.38	1.56	0	0	0.07	0	0	0	0
Vulturine Guinea-Fowl[a]	*Acryllium vulturinium*	23.9	—	99.50	0.46	0.04	0	0	0	0	0	0
Javan Hill Partridge[b]	*Arborophila javanica*	6.0	—	98.60	1.40	0	0	0	0	0	0	0
Reeve's Pheasant[a]	*Syrmaticus reevesii*	20.5	—	97.40	2.17	0.41	0	0.02	0	0	0	0
Rothschild's Peacock-Pheasant[b]	*Polyplectron inopinatum*	4.2	—	91.67	2.67	0.33	0	0.56	0	0	4.78	0
Indian Blue Peafowl[a]	*Pavo cristatus*	14.9	—	83.22	1.34	0.47	0.20	0.67	0	0	14.09	0
Himalayan Snowcock[b]	*Tetraogallus himalayensis*	10.3	—	97.89	1.30	0.81	0	0	0	0	0	0
Red Junglefowl[a]	*Gallus gallus*	9.8	—	97.58	1.95	0.28	0	0.19	0	0	0	0
Ruddy Duck	*Oxyura jamaicensis*	23.1	9.2	93.28	4.11	0.10	0.80	1.72	0	0	0	0
Whooper Swan	*Cygnus cygnus*	20.1	11.1	94.29	2.18	0.41	2.67	0.44	0	0	0	0
Tufted Duck	*Aythya fuligula*	21.2	7.4	95.69	1.98	0.74	0.64	0.94	0	0	0	0
Eurasian Wigeon	*Anas penelope*	19.0	9.0	98.47	0.42	0.22	0.58	0.31	0	0	0	0
Northern Pintail	*Anas acuta*	21.0	10.9	95.99	0.90	0.77	1.39	0.95	0	0	0	0
Mallard[b]	*Anas platyrhynchos*	8.7	—	85.55	4.52	0.74	3.13	0	0	6.06	0	0
Mandarin Duck[a]	*Aix galericulata*	14.1	—	92.33	2.03	0.62	1.64	0.49	0	2.88	0	0
Snowy Owl	*Nyctea scandiaca*	6.6	3.3	94.98	1.60	2.61	0	0.80	0	0	0	0
Sparkling Violet-ear	*Colibri coruscans*	7.1	3.0	93.81	3.31	0.86	0	2.03	0	0	0	0
Common Crane	*Grus grus*	20.8	12.7	98.07	0.94	0.56	0.40	0.03	0	0	0	0
White-naped Crane[b]	*Grus vipio*	20.7	—	93.67	4.41	0.94	0.85	0.13	0	0	0	0
Grey-necked Crowned-Crane[a]	*Balearica regulorum*	31.7	—	96.16	1.02	2.37	0.42	0.03	0	0	0	0
Lesser Black-backed Gull	*Larus fuscus*	26.0	15.0	—	—	—	—	—	—	—	—	—
Greater Flamingo	*Phoenicopterus ruber*	32.0	14.2	93.49	1.15	0.28	4.20	0.88	0	0	0	0
Scarlet Ibis[b]	*Eudocimus ruber*	21.6	—	99.57	0.24	0.11	0	0.09	0	0	0	0
Bald Ibis[a]	*Geronticus eremita*	23.9	—	95.96	2.03	0.12	0	0.10	0	0	0	1.80
Straw-necked Ibis	*Threskiornis spinicollis*	17.9	6.7	98.97	0.28	0.36	0.26	0.12	0	0	0	0
White Tailed Jay[b]	*Cyanocorax mystacalis*	4.3	—	89.24	6.82	1.81	1.60	0.53	0	0	0	0
Blue Magpie[a]	*Urocissa erythrorhyncha*	2.8	—	86.95	1.96	1.14	0	0.98	8.97	0	0	0
Mean		15.75	8.66	94.90	1.90	0.70	0.68	0.43	0.32	0.32	0.67	0.06
SE		1.58	1.28	0.82	0.29	0.14	0.20	0.10	0.32	0.24	0.53	0.06

[a] Indicates ornamental species.

[b] Indicates non-ornamental species.

Captive data are original, except in the case of *Larus fuscus* (Delius, 1988), *Pavo cristatus* (Walther, 2003), and *Struthio camelus*, for which we used combined original and published data (Deeming, 1998; McKeegan and Deeming, 1997). Wild data were all taken from publications (see Methods). For uniformity, only original data were used for *Struthio camelus* in the ornamental/non-ornamental comparisons (see Figure 4). Different types of maintenance are indicated by: P = preen, S = scratch, ST = stretch wings and tail, WH = wipe head, SR = shake and ruffle feathers, R = rub bill and head, B = bathe, D = dust, SU = sun.

behavior evolved as a response to evolutionary changes in plumage and other morphological traits. Instead of using species as individual data points, it is more informative to determine independent evolutionary events that confirm that the traits of interest have coevolved on several occassions (Nee et al., 1996; Read and Nee, 1995). Phylogenetically controlled analyses also have lower type I and II errors than across-species analyses (Harvey and Rambaut, 1998), and they control for the possibility of pseudoreplication, since related species could share the same unknown third variable that drives spurious correlations (Harvey and Pagel, 1991).

For statistical analysis of continuous species data (morphological variables), we used Model 1 multiple regression. Regression models were generated by subjecting an initial regression to a backward elimination procedure that omitted nonsignificant variables ($p > .05$; Sokal and Rohlf, 1995). All p values are two-tailed. For the phylogenetically controlled analyses, we calculated phylogenetically independent contrasts using methods developed by Felsenstein (1985, 1988), Harvey and Pagel (1991), and Pagel (1992). We used the program CAIC (Purvis and Rambaut, 1995), which generates independent contrasts for the variables being analyzed at each node within a phylogeny. Variables were subjected to Box-Cox transformation (Krebs, 1999) prior to CAIC calculations. Adequate standardization of each variable was tested by plotting the absolute values of the standardized contrasts against (1) their standard deviations and (2) the ages of the corresponding nodes (for a detailed description of the use of standardized contrasts see Freckleton, 2000; Garland et al., 1992; Harvey and Pagel, 1991; Purvis and Rambaut, 1994). We tested for association between continuous variables using Model 1 multiple regression fitted through the origin (Garland et al., 1992; Grafen, 1989).

For statistical analysis of binary species data (ornamental versus non-ornamental), we used one-sample sign tests and a permutation test for paired replicates (Siegel and Castellan, 1988) to test for differences between related taxa (Burt, 1989; Read and Nee, 1995).

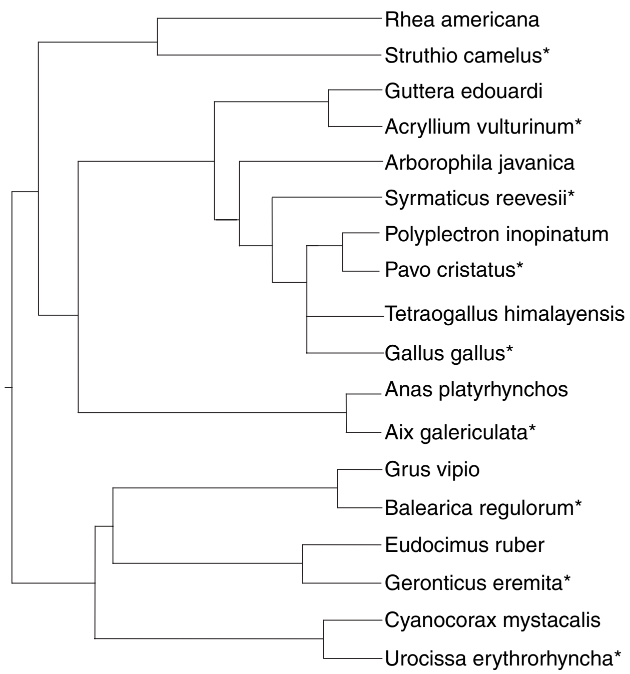

Figure 1
Phylogeny of the 18 species for which maintenance times of ornamental and non-ornamental related taxa were compared. Asterisks denote ornamental species. See Table 1 for common names.

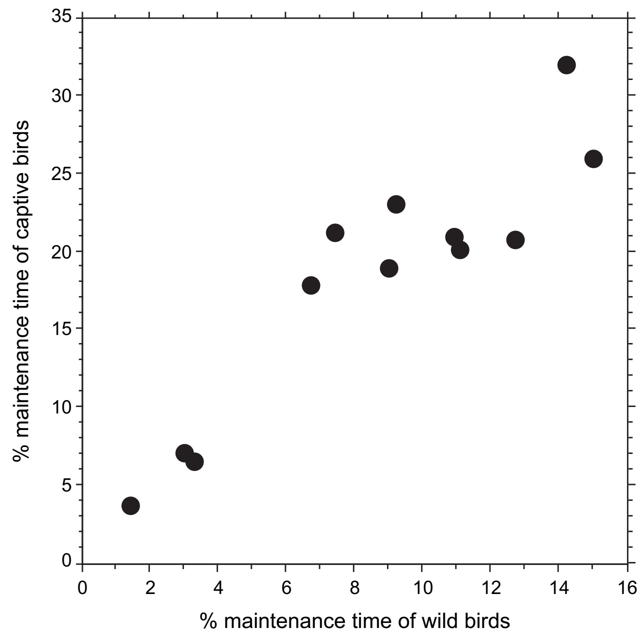

Figure 2
Comparison of % of daylight hours spent in maintenance behavior by wild versus captive birds (for species data, see Table 1; Model 1 regression, $n = 12$ species, $r^2 = .85$, $F = 56.11$, $p < .0001$). Note different scales of the two axes.

The phylogeny used for the comparative analyses (Figure 1) was derived from Sibley and Ahlquist (1990) and a more detailed phylogeny for the Phasianidae (Crowe, 2000).

RESULTS

Maintenance times of wild and captive birds

Preening was by far the most prevalent maintenance behavior in captive birds (Table 1). All other components of maintenance were displayed either rarely or were of very short duration. This presumably explains why preening was observed in all species, while other maintenance behaviors were not observed in some species. However, the absence of bathing, dusting, and sunning in many species may have been due to the lack of suitable water, dust, or sunlight in some enclosures, which may also explain the absence of shake-ruffling in five species. Shake-ruffling typically accompanies or follows bathing, dusting, and sunning (Simmons, 1964, 1985).

Maintenance times of species observed in the wild averaged 92.6% grooming (= preening, scratching, wiping, and head rubbing), 6.4% bathing, and 1% for other behaviors (Cotgreave and Clayton, 1994), while maintenance times of 29 captive species averaged 94.6% grooming, 0.3% bathing, and 5.1% for other behaviors (Table 1). The difference in bathing is due to the fact that many of the captive bird species had no access to water for bathing.

Among the 12 species for which we had data on both wild and captive birds, the captives spent about twice as much time, on average, in maintenance behavior (Table 1). Every species had higher maintenance times in captivity (one-sample sign test, $n = 12$ species, $p = .0005$). Despite the higher maintenance times of captives, the maintenance times of wild and captive birds were highly correlated (Figure 2). Hence, the relative amount of maintenance behavior among species was retained. In addition, the relative proportions of different maintenance behaviors were similar for wild and captive birds (see above).

Morphological correlates of maintenance time in captive birds

Maintenance times for the 18 ornamental/non-ornamental species (Table 1) were correlated both with body mass ($n = 16$ contrasts, $r^2 = .29$, $p = .03$) and plumage length (Figure 3). However, when plumage length was entered together with body mass into a multiple regression model, body mass did not explain significant variation in maintenance times (partial $r^2 = .01$, partial $p = .48$), while plumage length remained significantly correlated with maintenance time (partial $r^2 = .49$, partial $p = .03$). Maintenance times were not correlated with any variables associated with bill or foot morphology.

Maintenance times of ornamental versus non-ornamental birds

Plumage length was greater in every ornamental species when compared to its non-ornamental sister species (one-sample sign test, $n = 9$, $p = .004$; permutation test, $p < .05$), while body mass was not significantly associated with ornaments (one-sample sign test, $n = 9$, $p = .51$; permutation test, $p > .05$).

Only six out of the nine ornamental species spent more time in maintenance than their non-ornamental sister species (one-sample sign test, $n = 9$, $p = .51$). However, the three comparisons in which the ornamental species did less maintenance (*Rhea americana – S. camelus, Tetraogallus himalayensis – G. gallus* and *C. mystacalis – U. erythrorhyncha*) showed the smallest differences between species (Figure 4). We therefore also analyzed the differences in maintenance time using a permutation test for paired replicates that takes the magnitude of the differences into account (Siegel and Castallan, 1988). This analysis showed that, overall, the ornamental species spent significantly more time in maintenance

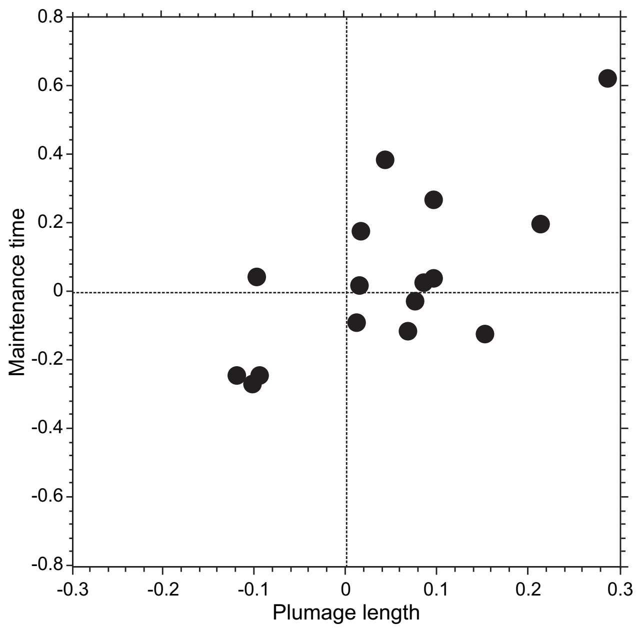

Figure 3
Plot of maintenance time versus plumage length (n = 16 contrasts, $r^2 = .49$, $F = 14.10$, $p = .002$) for 16 independent contrasts within the phylogeny (see Figure 1).

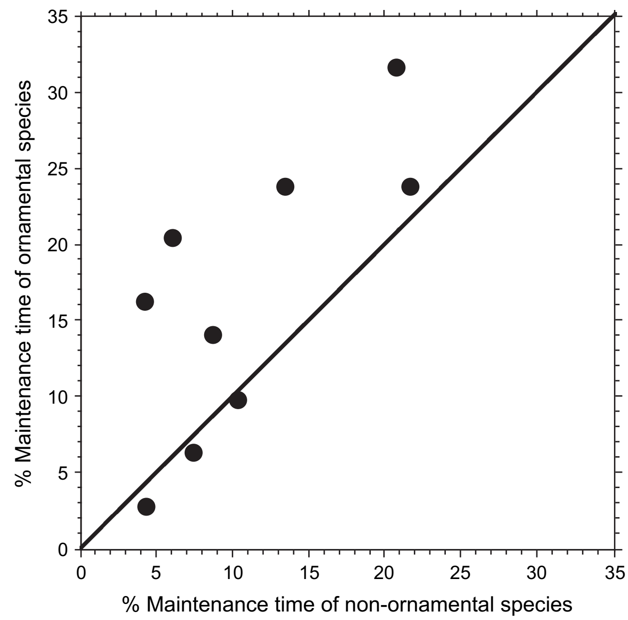

Figure 4
Plot of maintenance times of ornamental species versus non-ornamental sister species (n = 9 related taxa comparisons, permutation test, $p < .05$). Points above the diagonal line indicate that the ornamental species devotes more time to maintenance than its non-ornamental sister species.

behavior than the non-ornamental species (permutation test, $n = 9$, $p < .05$).

DISCUSSION

Preening was the most prevalent maintenance behavior in captive birds, with scratching being the second most prevalent behavior (Table 1). Similar results have been shown for wild birds (Clayton and Cotgreave, 1994; Cotgreave and Clayton, 1994; Simmons, 1964, 1985). Preening and scratching together accounted for more than 90% of maintenance time in both wild and captive birds, verifying the importance of the bill and feet as grooming tools (Clayton, 1991; Clayton and Cotgreave, 1994; Clayton and Walther, 2001). Despite this important role, however, none of our measures of bill or foot morphology correlated with maintenance time in this study. Thus, among-species variation in maintenance time could not be explained by variation in these traits.

Bouts of grooming often occur at regular intervals, suggesting intrinsic regulatory mechanisms (Delius, 1988; Greer and Capecchi, 2002). In contrast, irregular maintenance behaviors, such as bathing, dusting, sunning, and anting are often triggered by external stimuli (Borchelt, 1975; Cade, 1973; Delius, 1988; Lustick et al., 1978). Many of these behaviors are infrequent in wild birds and, not surprisingly, were not observed in all species of captive birds (Table 1). In some cases, the absence of a particular behavior may have been due to the absence of an appropriate stimulus, such as water for bathing. Our results showed that, although captive birds devoted twice as much time to maintenance as wild birds, relative maintenance times among species were strikingly similar in the two groups (Figure 2), a result previously found in ungulates (Hart et al., 1992). Captive birds may spend more time overall on maintenance behaviors because they are largely freed from the constraints of foraging and vigilance, which take up a substantial proportion of their daily time budgets in the wild. The strong correlation between maintenance times of wild and captive birds (Figure 2) enabled us to test the high maintenance hypothesis using captive birds alone.

Captive species with longer overall plumage had higher maintenance times than related species with shorter plumage (Figure 3). This correlation was not explained by body size covarying with plumage length, since body mass did not explain a significant amount of variation when entered together with plumage length in a multiple regression. Species with longer plumage spent more time on maintenance, independent of body size. Hence, among species of equal body mass, those with longer plumage have higher maintenance times, all else being equal. We refrained from using a measure of plumage length controlled for body mass (e.g., plumage length divided by body mass) because body mass could conceivably have independently influenced maintenance times. Larger birds could groom more because they have to maintain a larger number of feathers, even if feathers are of equal length in all species. Therefore, it was important to enter both variables independently.

Of course, body size is not the only variable other than plumage length that may influence maintenance time. For example, ectoparasite load can have a dramatic impact on grooming rates (Clayton, 1991; Moyer et al., in press). Air temperature and other environmental stimuli, such as the presence of conspecifics, may also influence when and how much birds groom (Delius, 1988; Simmons, 1986; Walsberg, 1983). Although our analyses could have included other variables such as ectoparasite load, air temperature, solar irradiation, and group size, we decided to concentrate on morphological variables because our original hypothesis focuses on a morphological trait.

All ornamental species had longer plumage than the non-ornamental related taxa. However, not all of the ornamental species spent more time in maintenance (Figure 4). In three of nine cases, the non-ornamental species devoted more time to maintenance. However, these three cases included the smallest differences in time, ranging from 0.5% to 1.5% (mean 1%). The six cases in which the ornamental species devoted more time to maintenance had differences ranging from 2.3% to 14.55% (mean = 9.3%). These cases included some rather large increases, such as the nearly fourfold greater maintenance time of peafowl (*Pavo cristatus*) compared to the peacock-pheasant (*Polyplectron inopinatum*) (Table 1).

One possible explanation for cases in which the non-ornamental species spent slightly more time on maintenance than the ornamental species may be the level of dimorphism among species. However, the three relevant comparisons involved two dimorphic species (*R. americana* – *S. camelus*), one monomorphic and one dimorphic species (*T. himalayensis* – *G. gallus*), and two monomorphic species (*C. mystacalis* – *U. erythrorhyncha*). Furthermore, the six comparisons that supported our hypothesis also involved a mix of the three possible combinations of monomorphic and dimorphic species (2, 1, and 3, respectively). Hence, there appears to be no trend related to level of dimorphism. Furthermore, the high maintenance hypothesis does not rely on the assumption that ornamental plumage is dimorphic, because both sexes may pay the high cost of maintaining ornamental plumage.

Four of the ornamental species were monomorphic (*A. vulturinum*, *B. regulorum*, *G. eremita*, and *U. erythrorhyncha*). These species may not be subject to the same intensity of sexual selection as the dimorphic species, although sexual selection may be acting on both males and females in these species. Although we assume that the target of sexual selection is the ornamental plumage, leading to an increase in preening, it is at least conceivable that the target of sexual selection is preening itself, leading to the evolution of "something to preen." Our comparative data cannot establish the direction of the causal arrow with certainty. Our analyses merely confirm that, regardless of the target, intensity, and direction of sexual selection, ornamental species devote significantly more time to maintenance behavior than non-ornamental species. Hence, ornaments are time consuming to maintain, which means they will invoke a cost, given the time constraints faced by wild birds.

Our results suggest that birds with ornamental plumage incur not only the initial cost of producing ornaments, but also a daily cost in terms of maintaining them. For example, peacocks spend a quarter of their total grooming time preening their trains (Walther, 2003). These maintenance costs should reinforce the honesty of ornamental plumage as an indicator signal (Andersson, 1994). While the mere presence of an ornament indicates that its bearer was healthy and vigorous at the time the ornament was produced, the presence of a well-maintained ornament shows that its bearer is capable of the day-to-day investment required to maintain the ornament in good condition. Hence, high maintenance traits convey honest information about current physiological condition.

Our results further suggest that high maintenance handicaps may also exist in taxa other than birds. For example, showy insects may need to groom more to keep their ornaments in good condition. Comparisons of the grooming times of ornamental and non-ornamental insects would be informative. Ornamental traits could even have community level effects. For example, such traits may select for cleaning symbioses in marine fishes (Barber et al., 2000), mammals (Murray, 1990), and other taxa that solicit help from other species in keeping their integuments in good condition. It would be interesting to compare the frequency of cleaning symbiosis for ornamental and non-ornamental species.

In summary, we have shown that the time wild and captive birds spend on maintenance behavior is correlated, even though captive birds spend twice as much time as wild birds. Among captive birds, we observed that species with longer plumage spend more time on maintenance, even after controlling for body mass. Ornamental species have more plumage, and they spend more time in maintenance behavior than non-ornamental species. These results provide support for the existence of high maintenance handicaps in birds. Such handicaps may also occur in other animals.

We would like to express our gratitude to the following people and institutions for access to their bird collections: Simon Blackwell, Assistant Curator at Cotswold Wild Life Park, Burford, Oxfordshire, UK; David Coles, Bird Curator at Beale Park, Child-Beale Trust, Church Farm, Reading, UK; Birdland, Bourton-on-the-Water; London Zoo, UK; Vogelpark Walsrode, Walsrode, Germany; and Brian Miller, Richard Reading, and Mary Susanne Wisz, Denver Zoo, Denver, Colorado, USA. We especially thank Nikki Collis and Anne Schuckman for help collecting data for captive birds and Karl Schuchmann for providing data on hummingbirds. We also thank Robert Prŷs-Jones for help at the Natural History Museum, Tring, UK and Linda Birch at the Edward-Grey-Institute library, Zoology Department, Oxford University, Oxford, UK. Finally, we thank Catherine Clarebrough, Timothy Crowe, Robert McCall, David Milson, Mark Pagel, Marion Petrie, Andy Purvis, Andy Rambaut, Andrew Read, Dan Tompkins, Graham Wragg, the late Paul Bühler, and three anonymous reviewers for providing valuable comments at various stages in the preparation of this paper. B.A.W. was supported by an Evan Carroll Commager Fellowship and a John Woodruff Simpson Fellowship from Amherst College, USA. D.H.C. was supported by National Science Foundation grants DEB-0107947 and DEB-0118794.

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