

Do peacocks devote maintenance time to their ornamental plumage? Time budgets of male blue peafowl *Pavo cristatus*

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Abstract

Elaborate secondary sexual traits, such as the ornamental plumage of birds, appear to be favoured by female choice because they serve as honest advertisements of male quality. Elaborate plumage is thought to be an honest signal because it is energetically expensive to produce and to carry, and it may also increase the vulnerability of males to predators. According to several recent studies, the elaborate ornamental train of male blue peafowls (*Pavo cristatus*) appears to be such an honest signal. In this paper, I explore another potential cost of such plumage, which is the daily time and energy investment required to maintain the plumage in good condition. Since time devoted to maintenance cannot be devoted to feeding, vigilance, or other activities, the maintenance cost of ornamental plumage should reinforce the honesty of such plumage as an advertisement of male quality. I observed free-ranging peacocks for 30 hours at the Denver Zoo in June 2002 and April 2003. Preening, scratching and dusting took up more than 99% of maintenance time. Long bouts of maintenance behaviour were performed while peacocks were resting or standing, while short bouts occurred while peacocks were walking or feeding. No maintenance behaviours were observed while peacocks displayed their trains. Peacocks spent 14.9% of their total time budget on maintenance behaviours and 7.2% on displaying their trains, and 25.2% of their total grooming time on preening their trains. Consequently, peacocks not only incur the costs of producing and carrying their trains, but they also pay an additional maintenance cost. Hypotheses concerning the indicator mechanism of ornamental plumage need to consider these additional costs, as any additional cost should make the signal even more "honest".

Keywords: *Pavo cristatus*, time budget, maintenance behaviour, grooming, sexual selection, indicator traits.

Introduction

Elaborate secondary sexual traits, such as the proverbial peacock's train, are assumed to provide females with honest information about male quality (Andersson, 1994). The honesty of such signals is thought to be reinforced by physiological costs associated with the production of the trait, as well as energetic costs associated with carrying the trait once it is produced. The additional weight and restraints to mobility may also make males more vulnerable to predators. Another relatively unexplored cost of ornamental traits is the need to maintain them in good condition. Birds devote a significant amount of time on maintenance behaviours, including preening, scratching, bathing, dusting, sunning, shaking, and ruffling of the feathers (Simmons, 1964; 1985; Walther, 1997; Moyer et al., 2003). Maintenance behaviours require energy (Croll & McLaren, 1993) and take time. Time and energy devoted to maintenance cannot be devoted to feeding, vigilance, or other

activities (Redpath, 1988). Nevertheless, all species of birds engage in maintenance, spending an average of 9.2% of their diurnal time budgets on these behaviours (Cotgreave & Clayton, 1994). The need to maintain ornamental plumage may therefore be another cost reinforcing the honesty of such traits as signals. A recent study comparing ornamental with non-ornamental bird species showed that ornamental species devote significantly more time to maintenance behaviours than non-ornamental species (Walther & Clayton, unpublished data). However, because of its sampling methodology, this study was not able to answer the question whether the additional time devoted to grooming by ornamental species was actually directed towards the additional ornamental plumage or just to the plumage in general.

Therefore, I chose to observe males of one of the quintessential ornamental species, the Indian blue peafowl *Pavo cristatus* (L.), to determine how much of their diurnal time budget is devoted to maintenance behaviours, and how much of the maintenance time is devoted to grooming the ornamental train. The ornamental train appears to function as an honest signal (Andersson, 1994), as peacocks with more elaborate trains are in better body condition (Petrie et al., 1996), suffer lower predation (Petrie, 1992), enjoy higher

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mating success (Petrie & Cotgreave, 1991 and Petrie & Halliday, 1994), and sire more offspring with higher viability (Petrie & Williams, 1993 and Petrie, 1994). Only two time budget studies of the blue peafowl have, to my knowledge, been published (Ridley et al., 1983-1984 and Sathyanarayana & Rathinasabapathy, 1990-1992), of which only the latter one enumerated preening as a behavioural category but without providing any other detail. Thus knowledge about the peafowl's maintenance behaviours is scant, and only vague statements may be found, e.g. that during the hot midday hours the species spends much of its resting time inside thick scrub to preen (Sathyanarayana & Rathinasabapathy, 1990-1992), or that it "goes into the forest where it will spend the hottest hours in the middle of the day, busying itself much of the time with the tasks of preening and dust-bathing" (McGowan, 1994).

The blue peafowl is highly dimorphic with females only weighing between 2.8 – 4 kg, while males weigh between 4 – 6 kg (McGowan, 1994 and Madge & McGowan, 2002). Furthermore, females lack the males' striking blue-green colouration and the highly ornate train that is actually not formed by the rectrices, which are dull coloured and of moderate size, but by the uppertail coverts. These coverts may reach 1.6 m length, and their spectacular appearance is created by disintegrated barbs and large subterminal ocelli. This species has its natural distribution in the Indian subcontinent, where mostly sedentary populations are found in semi-open habitats such as open forests and plains, scrubland, secondary vegetation, orchards and other cultivation near villages, usually near streams (McGowan, 1994 and Madge & McGowan, 2002). However, many feral populations have been established around the world in suitable locations. One such population is located in the Denver Zoo where the blue peafowl was first exhibited in 1911 (Etter & Etter, 1995, p.38). This founding population had grown to about 64 birds in late summer of 1999, with a sex ratio of about one male to two females (the population was censused at dusk when almost all birds roosted in leafless trees; D. Crawford, pers. commun.). The birds were free-ranging within the confines of the zoo (about 25 ha), walking and feeding inside and outside the animal enclosures, using trees and bushes for roosting and breeding, and open areas for displaying. I observed these free-ranging peacocks to determine how much of their diurnal time budget is devoted to maintenance behaviours, and how much of the maintenance time is devoted to grooming the ornamental train.

Material and Methods

I observed adult male birds in Denver Zoo for a total of 30 hours in June 2002 and April 2003 between 5:50 and 20:00 h. Focal animal sampling was used to collect behavioural data for male birds (Altmann, 1974). To ensure observation of different males, different parts of the zoo were visited, each about 100 m apart. Since many males maintained territories, this distance ensured that, in most cases, different males were observed. Upon reaching a part of the zoo, the focal animal was chosen as follows: it was either the first visible male, or, if several males were visible, a random number from 1 to 50 was chosen, then all males were counted from the left to the right (several times if necessary) until the random number was reached (Altmann, 1974). Recording of behavioural data began as soon as the fo-

cal male was spotted, and ended 60 minutes later, or when the male disappeared from sight. All observed males had fully grown trains (> 1 m length). The duration of each of the following general behaviours was recorded with a stopwatch:

Resting: when the bird was tugging its legs under its body, and the body was resting on the ground or on a branch, the bird was assumed to be resting.

Standing: when the bird was standing on the ground or on an elevated perch without moving.

Walking: when the bird was walking, but not feeding.

Feeding: when the bird was walking around in search of food, pecking at food items on the ground as they were encountered.

Displaying: when the bird was displaying its train, often by shivering it, and sometimes moving in slow circles.

During each of these general behaviours, I also recorded the time spent on the following maintenance behaviours: preening, scratching, wing stretching, head wiping, dusting, shaking and ruffling the feathers (Simmons, 1964; 1985 and Walther, 1997). Head wiping always involved wiping the head on the bird's back. Three maintenance behaviours were never observed: bill and head rubbing, bathing and sunning. In most cases I was also able to record which body part was groomed. I distinguished between grooming the head by scratching with the feet and grooming the rest of the body by preening with the bill. Body parts preened included the back, the wings, the train (including both rectrices and uppertail coverts), the body parts covered with blue and blue-green feathers (neck, breast, shoulders, flanks, and belly), and the feet.

Results

Males spent most of their diurnal time budget standing around (Tab. 1). Often, they stood on some elevated perch, like a fallen log, a fence or a tree branch. Although they may have rested, they were usually rather attentive, surveying their surroundings and frequently calling. Moreover, they spent about one-fourth of their standing time on maintenance behaviours. The second most prevalent behaviour was feeding, while walking without feeding only took up a small part of the total time budget. Resting was the third most prevalent behaviour and was, like standing, also frequently used for maintenance behaviours. Displaying took up about 7% of the total time budget, and was the most absorbing behaviour as no feeding or maintenance behaviour was performed during displays.

The five general behaviours could be put into three groups using the amount of maintenance behaviours (Tab. 1). The first group includes only displaying behaviour which required total absorption, so that no time was devoted to maintenance behaviours (or any other activity such as feeding). The second group consists of walking and feeding, which were only interrupted for short bouts of maintenance behaviours, probably as a result of some actual skin irritation (see Discussion). Wing-stretching and dusting did not occur in this group, whereby the absence of dusting is not surprising, as dusting usually involves lying down (see below). The third group consists of standing and resting, which were both used for long bouts of maintenance behaviours. For example, one male dusted its body for at least 33 minutes (since recording was

Table 1 - Percentage of time spent on various behaviours by peacocks during 30 hours of observation. The second column gives the percentage of time spent on five general behaviours (which add up to 100%). The following eight columns give the percentage of time spent on seven different maintenance behaviours and the total percentage of time spent on maintenance behaviours performed during each general behaviour given in the second column (e.g. during the 22.9% that birds were resting, they spent 3.6% on maintenance behaviour and the remaining 19.3% on just resting).

| behaviour | % time | % preen | % allopreen | % scratch | % dust | % wing stretch | % head wipe | % shake and ruffle | % maintenance behaviour total |
|-----------|--------|---------|-------------|-----------|--------|----------------|-------------|--------------------|-------------------------------|
| display | 7.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| feed | 25.8 | 0.4 | 0.0 | 0.1 | 0.0 | 0.0 | 0.004 | 0.02 | 0.52 |
| stand | 42.0 | 10.5 | 0.03 | 0.1 | 0.0 | 0.07 | 0.002 | 0.04 | 10.74 |
| rest | 22.9 | 1.5 | 0.0 | 0.0 | 2.1 | 0.0 | 0.02 | 0.0 | 3.62 |
| walk | 2.1 | 0.005 | 0.0 | 0.006 | 0.0 | 0.0 | 0.0 | 0.002 | 0.01 |
| total | 100.0 | 12.4 | 0.03 | 0.2 | 2.1 | 0.07 | 0.03 | 0.1 | 14.9 |

ceased after 33 minutes, the dusting bout may have even taken up to an hour) by digging a small pit into the sandy ground, then lying in it and starting to throw sand into its plumage with its feet and beak, and finally distributing the sand among its feathers with shaking and ruffling movements. Likewise, preening bouts lasted typically from a few minutes to up to an hour. However, such bouts were always interrupted by periods of looking up, so that only about half of the time was actually devoted to maintenance. These three groups differ significantly in the frequency and duration of grooming bouts (Friedman's test, $n = 638$ bouts of maintenance behaviour, $\chi^2 = 103.7$, $p < 0.0001$).

As has been shown for many other species (Clayton & Cotgreave, 1994; Walther, 1997 and Walther & Clayton, unpublished data), preening was by far the most important maintenance behaviour (Tab. 1). While in many other species scratching is the second most prevalent maintenance behaviour (Clayton & Cotgreave, 1994; Walther, 1997 and Walther & Clayton, unpublished data), the blue peafowl devoted more time to dusting than scratching. However, while dusting was only observed once but took up a long time period, scratching was observed frequently, but for very short periods of time ($n = 108$ observations, mean ± 1 S.E. = 2.8 ± 0.2 seconds, range 1 – 8 seconds). All other maintenance behaviours were typically only rarely performed and for very short periods (wing stretching: $n = 13$ observations, mean ± 1 S.E. = 5.3 ± 0.8 seconds, range 3 – 10 seconds; shaking and ruffling: $n = 19$ observations, mean ± 1 S.E. = 2.1 ± 0.1 seconds, range 1 – 3 seconds; head wiping: $n = 21$ observations, mean ± 1 S.E. = 1.1 ± 0.1 seconds, range 1 – 2 seconds). On two occasions, a female allopreened the focal male's feathers surrounding the eye ($n = 2$ observations, mean ± 1 S.E. = 12.5 ± 7.5 seconds, range 5 – 20 seconds).

Males spent almost two-thirds (63.0%) of their grooming time preening the wings, neck, breast, shoulders, flanks, and belly, while only about 7.5% of grooming time was devoted to the back (I assume here and in the following text that the undetermined category in Table 2 is equally divided among the other categories). Very little time was spent on the head (which can only be scratched) and the feet (which need little attention because they are featherless). About one-fourth (25.2%) of the grooming time was devoted to preening the train (or 3.2% of

Table 2 - Percentage of grooming time spent on various body parts by peacocks. Table 1 showed that males spent 12.6% on grooming (0.2% scratching the head with the feet and 12.4% preening the rest of the body with the bill). This table shows how these 12.6% were subdivided among different body parts (whereby undetermined means that no information was recorded on body parts either because the body part that the observed bird was grooming was not visible from my point of view or because the observed bird was changing between body parts too rapidly for records to be made).

| body part | % time |
|--|--------|
| head | 2.36 |
| neck, breast, shoulders, flanks, and belly | 25.27 |
| back | 5.67 |
| wings | 22.39 |
| train | 19.05 |
| feet | 0.96 |
| undetermined | 24.30 |

the total diurnal time budget). Interestingly, males spend so much of their grooming time preening their trains even though they were only able to reach the parts of the train feathers that are close to the body, as the more terminal parts of the train feathers (about three-fourths) were out of reach of the bill. An indication that preening the train may be important for displaying to females is that in one-fourth of all cases (4 out of 16) when a male displayed its train to females, a bout of train preening lasting between 10 - 25 seconds immediately preceded the display.

Discussion

Peacocks spent 42% of their daily time budgets standing (Tab. 1, first column), often on an elevated perch from which they survey their surroundings and regularly call. Peacocks may be resting or preening while standing, but they were usually actively surveying their territory for intruding conspecifics,

Table 3 - Time budgets by ¹Ridley et al. (1983-1984), ²Sathyanarayana and Rathinasabapathy (1990-1992) and ³this study. Empty fields are due to the respective study not recording that particular behavioural category. Note that the numbers in the last column correspond to the second column of Table 1 (“% time”) minus the last column of Table 1 (“% maintenance behaviour total”) except for “preening” which in this table subsumes all maintenance behaviours listed in Table 1 and “calling” which was subtracted from “standing” (since “calling” was not included as a behavioural category in Table 1).

| behaviour | % time budget ¹⁾ | % time budget ²⁾ | % time budget ³⁾ |
|------------|-----------------------------|-----------------------------|-----------------------------|
| displaying | 8.4 | 1.2 | 7.2 |
| perching | 8.3 | – | – |
| calling | 4.2 | 0.5 | 0.2 |
| feeding | 38.5 | 37.3 | 25.3 |
| standing | 23.5 | – | 31.0 |
| resting | 17.1 | 30.1 | 19.3 |
| walking | – | 19.1 | 2.1 |
| preening | – | 11.8 | 14.9 |

with the aim of chasing off other peacocks and displaying to peahens. Often, a male jumped from its perch and started displaying as soon as females approached. Unlike red junglefowl, which spent most of their time foraging and very little time resting (Dawkins, 1989), peacocks spent only about one quarter of their daily time budgets on feeding, but more than one-fifth on resting. Walking took up very little time, and displaying about 7% (Tab. 1).

These results can be compared to two other studies (Ridley et al., 1983-1984 and Sathyanarayana & Rathinasabapathy, 1990-1992). However, one crucial difference between these two studies and my study is that they recorded preening differently. For example, while I recorded whether a male was standing or resting while preening, Sathyanarayana & Rathinasabapathy (1990-1992) just recorded the male as preening, and Ridley et al. (1983-1984) just recorded the male as standing or resting. To make these studies somewhat comparable, I recalculated my results (Tab. 1) in a manner comparable to how the other two studies recorded behaviours (Tab. 3). Comparing the results (Tab. 3), it is evident that two studies recorded displaying as a regularly occurring behaviour, while Sathyanarayana & Rathinasabapathy (1990-1992) observed displaying only during one-hundredth of the time budget. This is partly due to them observing females as well as males, but still very surprising since the observation period (December through March) coincides with the reported breeding season (McGowan, 1994) so that one would expect males to display rather frequently. Ridley et al. (1983-1984) recorded considerably more calling than the other two studies. All studies agree, however, on that walking, feeding, standing and resting (including perching) are the main activities of peafowls. Moreover, both studies that enumerated preening agree that maintenance behaviours are an important part of the daily time budget of peafowls.

My observations differed from other published studies in a few other details. Hillgarth (1983-1984) and Ridley et al. (1983-1984) reported that males almost always displayed in secluded alcoves enclosed by bushes or walls. In the Denver Zoo, males displayed mostly in wide open spaces, e.g. on a large lawn (about 100 m x 100 m), which seemed to be the cen-

tral lek where often several males were displaying simultaneously. This difference may be due to the lack of appropriate alcoves or the lack of diurnal predators since Ridley et al. (1983-1984) suggested that hiding from predators may be one of the reasons for using alcoves. Also, while some males seemed to keep within certain territories, most males foraged widely within the zoo, crossing paths with many other males mostly without eliciting aggressive responses. Perhaps male density or food availability are so great at the Denver Zoo that it precludes the kind of territorial behaviour observed by Hillgarth (1983-1984), Ridley et al. (1983-1984) and Rands et al. (1984). Females and juvenile males moved widely and independent of the adult males in the zoo, often in flocks, thus supporting the view that the blue peafowl is a lekking and not a harem species (Hillgarth, 1983-1984; Ridley et al., 1983-1984 and Rands et al., 1984). Peafowl are omnivorous and take a wide selection of foods (McGowan, 1994). While they fed mainly on seeds (Sathyanarayana & Rathinasabapathy, 1990-1992), grass shoots and leaves, and some insects (Hillgarth, 1983-1984) in India, at Denver Zoo they ate a wide variety of plant materials, especially grass, but also anything edible that visitors gave them, including crackers, biscuits, and fruit.

Maintenance behaviours were unequally distributed among these different general behaviours (Tab. 1), and significantly so (see Results). Resting and standing were used for long bouts of maintenance taking up 96% of the total maintenance time (Tab. 1, last column). Probably because maintenance behaviours reduce vigilance (Redpath, 1988), they were often performed in secure locations, e.g. inside trees, on fence tops or under a bush (as in the case of the dusting bout described above). Therefore, some maintenance behaviours probably go undetected in time budget studies, unless individuals are always in the open (as ducks on lakes) or can be followed without being disturbed (as peacocks in zoos). However, even this study may have underestimated maintenance time because of the bias introduced by the initial choice of the focal animal (which may have overlooked any peacock hiding in dense vegetation). Walking and feeding, on the other hand, were general behaviours only interrupted by short bouts of maintenance

taking up the remaining 4% of the total maintenance time. Displaying seems to be a general behaviour that is so absorbing that peacocks never interrupted a display even for a short maintenance bout.

Thus, different general behaviours appear to be used for different types of maintenance bouts. Long bouts of maintenance behaviour are regularly performed behaviours that probably serve a prophylactic function keeping the plumage in good working order and removing dirt and ectoparasites (Simmons, 1964; 1985; Delius, 1988; Moyer & Clayton, 2003 and Moyer et al., 2003). Short bouts of maintenance behaviour, on the other hand, are usually reactive, as they most likely result from an actual skin irritation, e.g. a biting ectoparasite, and only last until the irritation has been removed (Delius, 1988). Different types of maintenance bouts have been observed in crested mynas (Nguyen-Clausen, 1975), budgerigars (Lefebvre, 1982), and kestrels (Lefebvre & Joly, 1982), where shorts grooming bouts occur with no predictable temporal pattern while long grooming bouts occur with some degree of periodic occurrence, suggesting that short bouts serve to deal with momentary peripheral irritations while long bouts serve a prophylactic function that is internally facilitated. The internal facilitation of long stereotyped grooming bouts is also supported by experiments. For example, praying mantis kept performing stereotyped grooming movements even though the behaviour had become non-functional after their forelegs had been amputated (Zack, 1978). Stereotyped grooming bouts can even be elicited by hormone injection or electrical stimulation of the brain (Delius, 1988 and Van Erp et al., 1991) and be impaired by brain damage due to surgical lesions (Cromwell & Berridge, 1996) or genetic mutations (Strazielle & Lalonde, 1998).

Preening, scratching and dusting took up more than 99% of maintenance time (Tab. 1). These maintenance behaviours are therefore much more important than the other maintenance behaviours such as wing stretching, head wiping and shaking and ruffling the feathers. These huge differences are most likely explained by the different functions of each maintenance behaviour. Preening with the bill is obviously the most efficient way of cleaning and rearranging the feathers, and the bill is the most efficient grooming tool that can reach most of the plumage (Peterson, 1993; Clayton & Walther, 2001; Moyer & Clayton, 2003 and Moyer et al., 2003). The feet, on the other hand, are less efficient grooming tools and only reach a small part of the plumage located on the head (Clayton & Cotgreave, 1994 and Moyer et al., 2003). Dusting (like bathing and sunning) alters the physical conditions of the plumage, and probably serves a similar function as grooming, i.e. cleaning the plumage and possibly destroying ectoparasites (Simmons, 1964; Simmons, 1985; Moyer & Clayton, 2003 and Moyer et al., 2003). Birds shake and ruffle only during dusting or bathing bouts to distribute sand or water in the plumage or at the end of a preening bout to put the feathers back into place. It thus has a much more limited applicability. Likewise, head wiping may only serve to distribute preen oil into the head plumage, and wing stretching may not even have a maintenance function but may rather be a comfort behaviour to stretch the muscles.

Peacocks spent 7.2% of their total time budget on displaying their trains (Tab. 1) and 25.2% of their total

grooming time on preening their trains (Tab. 2). Thus, a species with one of the most elaborate ornamental plumages not only spends a considerable amount of time displaying its ornamental plumage, but also pays a considerable maintenance cost. This cost may be especially high in fitness terms as grooming decreases vigilance (Redpath, 1988). However, it still needs to be shown that the maintenance cost associated with preening the ornamental plumage is actually higher than the cost associated with preening the non-ornamental equivalent, as non-ornamental species of course also preen their tail feathers. Such a study would compare the amount of grooming time directed towards the ornamental plumage and its non-ornamental equivalent in closely related sister taxa. However, given that ornamental species spent more time on maintenance directed at the entire plumage than non-ornamental sister species (Walther & Clayton, unpublished data), such an outcome seems probable.

Consequently, birds with ornamental plumage may not only incur the costs of producing and carrying their ornaments, but they may also pay an additional maintenance cost. Hypotheses concerning the indicator mechanism of ornamental plumage (Andersson, 1994) need to consider these additional costs, as any additional cost should make the signal even more "honest". Also, while the presence of an ornament may only indicate that its bearer was healthy and vigorous at the time the ornament was produced, the presence of a well-maintained ornament should indicate that its bearer is capable of the day-to-day investment required to maintain the plumage in good condition. Thus the present state of an ornament (and not just its presence) would indicate that its bearer is currently healthy and vigorous. Such an indicator allows females to assess not only the genetic quality of a potential mate, but also its current physiological condition. The studies by Petrie and others (cited in the Introduction) certainly suggest such an indicator function for the ornamental train of peacocks.

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