MOULT-BREEDING OVERLAP AND FECUNDITY LIMITATION IN TROPICAL BIRDS: A LINK WITH IMMUNITY?

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SUMMARY.—Moult-breeding overlap and fecundity limitation in tropical birds: a link with immunity?

Plumage moult is a costly maintenance process which conflicts with the requirements for breeding, explaining the avoidance of moult-breeding overlaps in many species. However, moult-breeding overlaps are especially frequent in the tropics, a fact which has been related to protracted breeding seasons and small clutches linked to high nest predation. Here, a new hypothesis explaining the high incidence of moult-breeding overlaps and low fecundity in tropical birds is proposed. Parasites and pathogens of birds may be more prevalent in the tropics than in temperate regions, requiring a higher level of immune responsiveness. There is observational and experimental evidence that moult interferes with immunity, and that the induction of an immune response delays the initiation of postnuptial moult. To avoid this conflict between a necessarily high preparedness of the immune system and plumage renewal, moult would have to be slowed down. Protracted moult processes would imply a high incidence of moult-breeding overlap. This, in turn, would reduce resources necessary for reproduction, leading to small clutches. Immunity and moult would limit fecundity in tropical birds.

Key words: Clutch size, immunity, life history trade-offs, moult-breeding overlap, tropics.

RESÚMEN.—¿Solapamiento muda-reproducción y limitaciones en fecundidad en aves tropicales: una conexión con la inmunidad?.

La muda del plumaje es un proceso costoso de mantenimiento que compite por los recursos necesarios para la reproducción, lo que explicaría por qué en muchas especies se evitan los solapamientos temporales entre muda y reproducción. Sin embargo, estos solapamientos son especialmente frecuentes en los trópicos, un hecho que se ha relacionado con temporadas prolongadas de cría y pequeñas puestas debido a la elevada depredación de nidos. Aquí se propone una nueva hipótesis para explicar la elevada incidencia de solapamientos muda-reproducción y la baja fecundidad en aves tropicales. Los parásitos y agentes patógenos pueden ser más prevalentes en los trópicos que en regiones templadas, lo que requeriría un nivel más elevado de respuesta inmunitaria. Existen evidencias observacionales y experimentales de que la muda interfere con la inmunidad, y de que la inducción de una respuesta inmunitaria retrasa el inicio de la muda postnupcial. Para evitar este conflicto entre una necesariamente elevada preparación del sistema inmunitario y la renovación del plumaje, la muda debería ralentizarse. Procesos prolongados de muda implicarían una alta incidencia de solapamiento muda-reproducción. Ello a su vez reduciría los recursos necesarios para la reproducción, lo que conllevaría puestas pequeñas. La inmunidad y la muda limitarían la fecundidad en aves tropicales.

Palabras clave: Compromisos de estrategias vitales, respuesta inmunitaria, solapamiento muda-reproducción, tamaño de puesta, trópicos.

Plumage moult is a costly maintenance process which induces changes in the energetic and nutritional needs of birds (Dietz et al., 1992; Klaassen, 1995; Murphy, 1996). It also involves important reallocations of resources among organs and functions (Murphy & Tarusco, 1995; Thompson & Drobney, 1996; Schieltz & Murphy, 1997; Fox & Kahlert, 1999; Nava et al., 2001) as well as increased vulnerability to predators (Haukioja, 1971; Slagsvold & Dale, 1996; Rivera et al., 1999; Lind, 2001) or a total impairment of foraging activities (Adams & Brown, 1990). Feather loss may impair flight performance (Swaddle et al., 1996; Swaddle & Witter, 1997; Chai, 1997; Swaddle et al., 1999) and thus make moult and reproduction incompatible (Langston & Rohwer, 1996). Accordingly, exposure to reproductive hormones may prevent moult (Keterson et al., 1996), and moult processes can be interrupted until the independence of young (Norman, 1998). The initiation of moult in

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some species is related to a decreased reproductive effort (Svensson & Nilsson, 1997; Siikamäki, 1998; Hemborg & Lundberg, 1998), which suggests that both processes are not easily compatible when functioning simultaneously. Also, experimentally increased reproductive effort impairs moult processes (Siikamäki et al., 1994; Klemp, 2000; but see Sanz, 1997; Hemborg & Merilä, 1999). Moult-breeding overlaps are thus inherently costly (Hemborg et al., 2001), which may explain their avoidance in most temperate species. Rapid moult may also be costly due to effects on feather quality (Nilsson & Svensson, 1996; Dawson et al., 2000; Hall & Fransson, 2000), implying that a considerable part of the annual cycle has to be devoted to moult (Rothery et al., 2001).

Moult-breeding overlap is more frequent in the tropics, and appears to be associated to protracted moult processes (Foster, 1974, 1975; Dittami, 1987; Savalli, 1993; Tidemann & Woinarski, 1994; but see Craig, 1996; Milingwa, 1996; Marini & Duraes, 2001). A protracted moult in the tropics may be the consequence of a longer period of high food availability allowing diversion of resources to moult, or to the absence of migratory processes which may interfere with moult for many temperate species (Rintamäki et al., 1995; Ogden & Stutchbury, 1996; Merilä, 1997). The high nest predation rates in the tropics (Skutch, 1949; Ricklefs, 1970) may select for the capacity to re-nest repeatedly throughout a prolonged breeding season. This may increase the probability of overlap given the constraints on rapid moult (Foster, 1974). According to this scenario, moult-breeding overlaps in the tropics would be the unavoidable consequence of prolonged breeding seasons and protracted moult processes. However, if moult-breeding overlaps involve problems for both reproduction and feather development as has been suggested, the question is why do not tropical birds with overlap compress moult to the same degree as temperate species in order to conserve a longer part of the yearly cycle only for reproductive activities. After all, many temperate species can concentrate their moult in a few weeks (Ginn & Melville, 1983), while many tropical species moult during periods of several months (Wyndham, 1981; Tidemann & Woinarski, 1994). Murphy (1996) has adequately stressed that rates of moult cannot be constrained nutritionally but must be subjected to trade-offs with other functions through hormonal links. The question arises as to which functions are those linked with moult through functional trade-offs.

Several not mutually exclusive explanations for why some tropical birds may have a protracted moult despite its costs can be envisaged:

1) Tropical birds may moult at a slow rate due to nutritional constraints,

2) Predators that may be avoided in flight may be more abundant or efficient in the tropics,

3) Tropical birds are in stronger need of a high-quality plumage due to climate,

4) The immune system may be more active in tropical species due to a stronger parasite pressure, and there may exist a moult-immune system activation trade-off.

The first possibility was contemplated to explain the low fecundity of tropical birds (Ricklefs, 1970; Owen, 1979), and is not easily dismissed. Frugivores, which are especially abundant in the tropics (Stutchbury & Morton, 2000), have protein-poor diets that do not allow rapid feather replacement. We would predict more protracted moult in frugivores compared to insectivores. Foster (1975) analyzed the feeding habitats of 121 tropical species with moult-breeding overlap without finding any association of degree of overlap with diet. Also, birds in the tropics may be subjected to higher predation risks which may preclude any impairment in flight capabilities. A prediction of this hypothesis is that protracted moult would be more prevalent in habitats with more aerial predators that select for high flight performance. Open habitats may require higher flight capabilities than closed ones. Again, Foster (1975) did not find any association of habitat type with moult-breeding overlap. Feathers may be degraded by bacteria and fungi, especially in hot and humid conditions which favour bacterial and fungal growth (Burtt & Ichida, 1999). Accordingly, species from mesic habitats would experience more protracted moult processes than those from arid conditions. This prediction is contradicted by the findings that individuals of the same species have a slower moult in dry than in humid areas (Payne, 1980; Schoepfer, 1989; Tidemann & Woinarski, 1994). Finally, the rearrangements in immune function which a rapid moult requires...
would be selected against in the tropics. Pathogens may be more frequent and severe in tropical latitudes (Janzen, 1970; Connell, 1971; Møller, 1998), requiring the maintenance of full immune capabilities. Møller (1998) has found evidence that tropical species invest more resources in the immune system. The first three hypotheses require proper comparative tests and merit further attention. None of the hypotheses presented are mutually exclusive. Here, I will concentrate on the last hypothesis given the scant attention devoted to the immune system in the literature on moult patterns and geographic variation in avian life histories.

Strong immune reactions may not be compatible with rapid moult due to competition for resources between the immune system and the developing feathers, or because the inflammatory reactions to pathogens may impair moult. There is evidence that induced moult in hens has a negative effect on the cellular component of the immune system (Holt, 1992). Also, recent experimental studies in the wild indicate that mounting an immune reaction delays the initiation of moult (Ilmonen et al., 2000; Sanz et al., 2004). Other growth processes in birds appear to be involved in trade-offs with immunity. Thus, rapid nestling growth apparently conflicts with investment in the immune system (Klasing et al., 1987; Fair et al., 1999; Soler et al., 2003). This may be due to a resource allocation trade-off between the immune system and other developing tissues and organs, or to the incompatibility between strong immune reactions and normal cell proliferation. Feather growth could be involved in a similar trade-off as juvenile growth. On the other hand, moult may induce increments in immune capacity associated to increased peripheral blood circulation and follicle development (Ward & D’Cruz, 1968; Silverin et al., 1999; Nava et al., 2001). Also, moult apparently interferes with the immunosuppression induced by high reproductive effort by inducing a stronger cell-mediated response (Moreno et al., 2001). This conflicting evidence suggests competition within the immune system between supporting expanded blood circulation and mounting attacks against pathogens, rather than between immunity and some other process.

Other possible interactions between moult and immunity concern the role of feather pigments. Thus, melanins strengthen feathers (Goldstein et al., 2004), but also have antioxidant properties (Rozanowska et al., 1999), which could benefit immune system functioning (Riley, 1992; Mackintosh, 2001). Another potential source of trade-offs is due to the fact that melanin synthesis depends on the use of tyrosine (Jawor & Breitwisch, 2003), an amino acid necessary for feather production (Murphy, 1996). Carotenoid pigments are antioxidants that enhance and modulate immune function (Møller et al., 2001) and are deposited in the plumage of many tropical species. If parasites are more virulent in the tropics, birds may use more pigments for enhancing immunity, leaving less for deposition in feathers. This could result in prolonged moult processes if pigmentation is strongly selected in the context of plumage quality enhancement or sexual attraction.

If the possibility of interactions between immunity and moult was confirmed, moult could constrain fecundity in the tropics through two mechanisms. First, given the need to extend moult temporally to avoid conflicts with immunity due to rapid moult, reproduction would necessarily overlap with moult. As hypothesized to explain the constraints on moult-breeding overlap at high latitudes, energy or nutrients needed for moult would be unavailable for sustaining an intense reproductive effort. Second, the adjustments of the immune system due to moult would be incompatible with the reproductive immunosuppression needed to avoid autoimmune disorders (Råberg et al., 1998). There is some evidence that moult interferes with normal immunosuppression during the nestling period in temperate passerines (Moreno et al., 2001). In this study, moult score was positively associated with the cell-mediated immune response. A reduced reproductive effort would reduce the risk of autoimmune disorders and make reproduction and moult simultaneously compatible. This possibility does not disclaim the importance of nest predation and relaying ability as constraints on clutch size of tropical birds (Foster, 1974), but would explain cases in which nest predation does not seem to explain low reproductive efforts (e.g. Martin et al., 2000).

There are three crucial links in this chain of arguments: 1) Parasite pressure should be higher in the tropics (Møller, 1998); 2) rapid moult should be incompatible with full immune capa-
city (Sanz et al., 2004), and 3) moult should interfere with immunosuppression associated to intense breeding effort (Moreno et al., 2001). The evidence for each of them is still scant, but should be possible to obtain. According to the proposed scenario, moult-breeding overlaps would not be a consequence of protracted breeding but of protracted moult imposed by immunity-moult trade-offs. Moult processes may constitute a crucial constraint on avian life histories in the tropics.

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