Essay

DIGESTIVE CONSTRAINTS AND LEKKING BEHAVIOR IN BIRDS

RESTRICCIONES DIGESTIVAS Y EL COMPORTAMIENTO REPRODUCTIVO DE "LEK" EN LAS AVES

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ABSTRACT

Males of lekking bird species can spend 80 - 90% of their time at leks. This paper addresses how these males can afford to dedicate such large portions of their time budgets to territorial and courtship activities without apparently compromising daily energy gains. A review shows that at least 94% of lekking bird species feed on fruits, nectar or foliage. The rate of food intake, and hence of energy acquisition, in these groups is likely limited by digestive and absorptive processes. I argue that such limitations have two important consequences for the evolution of lekking behavior in birds. First, they place a constraint on the energy budget by limiting the rate at which food can be assimilated. Second, they determine that most of the daily time budget must be used in digestion and absorption of the food. Under these constraints, I propose that lekking males devote time that would otherwise be spent in digestion to mate acquisition. Thus, they do not compromise their rate of energy acquisition. Similar principles may apply to other groups of lekking birds and to mammals. I conclude that the evolution of leks in birds and other vertebrates might be better understood by considering the constraints of food processing after ingestion.

Key words: leks, frugivorous birds, hummingbirds, tetraonids, fruit, nectar, foliage, digestive bottle-necks.

RESUMEN

Los machos de especies de aves formadoras de leks pueden pasar un 80-90 % de su tiempo en el lek. En este trabajo consideramos cómo estos machos pueden permitirse dedicar períodos tan extensos de tiempo a actividades territoriales y de cortejo sin comprometer aparentemente sus ganancias energéticas diarias. Una revisión demuestra que al menos 94% de las especies de aves que forman leks se alimentan de fruta, néctar o follaje. En estos grupos dietarios la tasa de ingesta del alimento, y por consiguiente la de adquisición de energía, es probable que están limitadas por procesos fisiológicos, tales como la digestión y la absorción y no por factores ecológicos como la disponibilidad del alimento. Proponemos que tal limitación puede tener dos consecuencias importantes para la evolución del comportamiento reproductivo de leks en las aves: Primero, establece un límite al tope superior del presupuesto energético al limitar la tasa a la cual el alimento puede ser asimilado. Segundo, determina que la mayor parte del presupuesto diario de tiempo debe ser usada en la digestión y absorción del alimento. Bajo estas restricciones, proponemos que los machos de las especies que hacen leks dedican un tiempo a la adquisición de parejas, que de otra manera hubiera sido dedicado simplemente a la digestión del alimento. Por lo tanto, los machos de aves formadoras de leks en realidad no comprometen su tasa de adquisición de energía. Principios similares pueden aplicarse a otros grupos de especies de aves y mamíferos formadoras de leks. Concluimos que la evolución de los leks en aves y otros vertebrados podría ser mejor comprendida considerando las restricciones impuestas por los procesos relacionados con el procesamiento del alimento después de su ingestión.

Palabras clave: leks, aves frugívoras, Trochilidae, Tetraoninae, fruta, néctar, follaje, cuellos de botella digestivos.

INTRODUCTION

Males of bird species that display at traditional display grounds, or leks, regularly spend 80% to 90% of their time on or near their display area (Snow 1963, 1976); e.g. during the breeding season, males of the Greater Praire-chicken (*Tympanuchus cupido*), a North American galliform, spend an average of 95 % of their time at the lek (Schoeder and Braum 1992) and males of Neotropical lekking manakins *M. manacus* (Snow 1962a) and *Pipra erytrocephala* (Snow 1962b) spend respectively 90% and 88% of daylight hours in the lek. Lekking behavior in tropical species can continue throughout the seven to nine month breeding season (e.g. Stiles and Wolf 1979, Levey and Stiles 1994).

Extended periods of time at the lek might be necessary for two reasons. First, intra-sexual competition is strong and prolonged male-male interactions are frequent and may define dominance relationships among males or be used by females as cues to select mates (Avery 1984, McDonald 1989a, Atwood, Fitz and Bamesberger 1991). The continuous singing and self-advertising of a male in his lek territory is an essential indication of ownership (Snow 1974). Second, the initial stages of courtship, leading to copulation, occur at the lek. Therefore, to maximize their chances of mating, males must be available whenever a receptive female arrives at the lek (Stiles and Wolf 1979). Consequently, one of the conditions necessary for the evolution of lek behavior is sufficient «free» time beyond that required for self-maintenance activities such as feeding (Snow 1962a, 1963). In fact, the evolution of leks is probably limited to species in which   males can devote most of their time to defense of the lek territory and to courting (Stiles and Wolf 1979).

Since lek territories seldom contain food resources, how can lekking birds afford to spend such large portions of their time budget at the leks? The existence of a relationship between a vegetable diet and promiscuous reproductive behavior has long been recognized (Snow 1962a, Lack 1968, Snow 1970, Beehler 1983,1989). Hence, David Snow (1962a, 1963) and Barbara Snow (1970, 1972) have convincingly argued that since fruit and nectar seem to be frequently abundant throughout the year and conspicuously advertised, lekking species of birds can use these resources to satisfy their food requirements in a short time.

Even if food is abundant, it seems paradoxical that lekking birds can allocate most of their time to territorial and courtship activities for extended periods of time without, in most cases, seriously compromising their daily energy gains (but see McDonald 1989b). I suggest that the amount of food consumed by lekking birds is constrained by a digestive bottle-neck. This is evolutionarily significant because once a bird's food processing time becomes a major part of its time budget and its food procurement time becomes a minimal part, it will be able to apportion digestion time simultaneously to other activities, such as self-advertisement. In addition, if food intake is limited by a digestive bottle-neck, then energy gains cannot be increased by increasing foraging time; thus while dedicating most of their time to display activities, lekking birds would not compromise their rate of energy acquisition.

Below I review the evidence suggesting that in several groups of lekking birds processing of the food may limit intake, and then discuss why process-rate limitations can have important implications on the evolution of lekking behavior. Finally I argue that to better understand lekking behavior it is important to consider processing strategies of the food.

In which dietary groups is food processing likely to be the step-limiting process in energy acquisition ?

The rate of conversion of food into usable energy can, in principle, be constrained by the maximum rate of foraging or of digestion and absorption (Weiner 1992). A widespread assumption is that birds are food limited (see Cody and Diamond 1975, Martin 1986, Wiens 1989 for general discussions). Nevertheless, there is a growing body of evidence indicating that energy

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acquisition in many species of birds might be limited, not by the rate at which they can encounter or capture food, but by the rate at which the energy and nutrients of the food are digested and absorbed in the digestive tract (Weiner 1992). Frugivores provide some of the best examples of limitation in consumption rate by digestive processes (Karasov and Levey 1990, Levey 1992).

Fruit-eating is predominant among lekking species of birds. Of approximately 130 species known to lek, or that show variations of the lek theme, at least 100 (77%; calculated from Payne 1984) feed predominantly or exclusively on fruit. These include members of phylogenetically unrelated families such as Cotingidae, Pipridae, Tyrannidae, Pycnonotidae, Paradisaeidae and Ptilonorhynchidae (Payne 1984, Trail 1990). Most fruit is energetically poor, nutritionally bulky and has a considerable portion of indigestible seed mass (Morton 1973, Stiles 1980, Moermond and Denslow 1985). Consequently, most specialized frugivores must eat daily amounts of fruit approaching double their body mass in order to subsist. Such high intake rates require that food move rapidly through the gut (Walsberg 1975, Herrera 1984, Moermond and Denslow 1985, Snow and Snow 1988, Worthington 1989, Karasov and Levey 1990, Levey and Karasov 1992).

Constraints imposed by gut volume coupled with rapid processing of large amounts of fruit seem to limit the rate at which food can be consumed by frugivorous birds (Karasov and Levey 1990). Levey and Grajal (1991) showed experimentally that Cedar Waxwings (*Bombycilla cedrodrum*) could eat more when they could void seeds faster, strongly implying that intake was limited by the rate at which the birds could process fruit in their guts. Furthermore, through image-intensification radiology, Levey and Duke (1992) showed that fruits stored in the esophagus moved into the gizzard only after the latter had been cleared from the previous meal, thus freeing the foregut for another meal.

Hummingbirds are the second largest group of lekking birds, c. 11% of all lekking species

(calculated from Payne 1984). In about half of the tropical species studied, males at least occasionally display in leks (Payne 1984). Nectar consumed by hummingbirds is, like fruit, a dilute foodstuff. In general, it has a low concentration of sugars (typically 20% dry mass, Baker 1975) and therefore a low energy content (on a fresh matter basis). On average it contains 3.3 kj/g fresh mass (estimated from table 2 in Karasov 1990 and assuming 20% dry matter), which makes it an energetically poorer foodstuff than most fruits (see table 2 in Karasov 1990). Consequently, to satisfy their high mass specific energy requirements hummingbirds must, like frugivores, process large amounts of food. Field measurements of water influx in hummingbirds show that daily nectar input easily exceeds body mass (Powers and Nagy 1988, Weathers and Stiles 1989, Tiebout and Nagy 1991). Hummingbirds -like frugivores- must process their food rapidly compared to most other vertebrates (e.g. Karasov *et al.* 1986).

Again, the need to rapidly process large amounts of food seems to limit ingestion rate in hummingbirds. Experimental evidence shows that in Anna's (*Calypte anna*) and Rufous (*Selasphorus rufus*) hummingbirds, feeding bout frequency is limited by crop-emptying time, which in turn is limited by intestinal nutrient absorption or by the time required for acidification of the stomach content (Diamond *et al.* 1986, Karasov *et al.* 1986).

Lekking behavior is also common among the Tetraoninae (grouse, ptarmigans), a sub-family of galliform birds that feeds extensively or exclusively on foliage, twigs and buds (Campbell and Lack 1985). In this group, eight of 15 species that have been studied (53%) form leks (Payne 1984). A large fraction of the energy content of herbage is locked up in the fibrous cell wall, only 7% - 35% of which can be digested by grouse (Remington 1989, Karasov 1990 and references therein). Grouse and related species are able to extract, on average, only about 37% of the energy available in their foodstuff. Therefore, the metabolizable energy that can be extracted per gram of herbage ranks lowest among bird's food (table 2 in Karasov 1990). On average, grouse and other herbivores must ingest almost three

times as much food mass as an insectivore or a carnivore to obtain the same amount of metabolizable energy (Karasov 1990).

Foliage, in addition to being bulky and energy dilute, might contain a number of secondary compounds that further hinder its utilization by animals (Levin 1976). Digestion of fibrous foliage is a complex process and it is not yet fully understood in grouse. Grouse nevertheless have an alternative strategy to that of frugivores and hummingbirds to deal with high bulk diet. They have large storage chambers in their guts where food is retained for long periods. The more digestible fraction of the digesta can be retained for up to a day in the large cecae (Gasaway *et al* 1975, Gasaway 1976b, Moss 1989) where bacterial fermentation of fiber, cell solubles or suspended material occurs (McBee and West 1969, Gasaway 1976a, 1976b, Remington 1989). The diluent effect of fiber and plant secondary compounds on metabolizable energy, coupled with the need to retain the digesta for long periods of time, can limit intake in grouse (Wittenberger 1978, Moss 1989, Remington 1989). Although the evidence is not conclusive it is proposed, largely by analogy with mammalian ruminants that ferment highly fibrous food, that digestion is the step limiting process in energy acquisition. Thus, in species of wild tetraonids that consume fiber-rich food, bulk is thought to limit intake (Moss 1989). In addition, Wittenberger (1978, 1981) has proposed that the rate at which secondary compounds can be detoxified limits the rate of food intake in grouse species that feed on conifer needles, which are abundant and contain large amounts of plant secondary compounds.

Why process-rate limitations may have important implications on the evolution of lekking behavior ?

Hence c. 94% of lekking species of birds (approximately 122 of 130; calculated from Payne 1984) belong to groups for which there is evidence that digestive and absorptive processes might limit the rate of food intake. Limitations caused by

processing rate might have two important implications for the evolution of lekking behavior. First, it places a constraint on the energy budget by limiting the rate at which food can be converted into usable energy. Second, it determines that a large portion (probably most) of the daily time budget must be used in digestion and absorption of food (e.g. Diamond *et al.* 1986).

These constraints in turn might allow lekking birds to allocate most of their available daylight hours to territorial and courtship lek behavior without seriously risking their energy intake. Most important, time used in the digestion of food could be simultaneously used in lekking, or in other activities (e.g. Courtney and Sallabanks 1992), without actually compromising the upper limit of energy acquisition. Under these constraints, rate of energy acquisition can not be increased by increasing the time dedicated to foraging. Hence lekking species of birds might actually be energy maximisers, rather than time minimisers (Schoener 1971, Diamond *et al.* 1986), as they could appear at first consideration. The time budget of lekking birds could be better explained by considering that they are not really compromising their rate of energy acquisition while displaying at leks. Instead, they are devoting digestion time to mate acquisition.

Why it is important to consider the constraints and consequences of food processing ?

For the benefit of simplicity, no distinction was made regarding potential differences in food consumed or in food handling characteristics of species belonging to each of the groups discussed above. Within any of these groups, exists a diversity of ecological situations that can produce varied responses in a bird's physiology or behavior. Those differences might in turn help to further explain the absence or presence of lekking behavior of species within groups. For instance, many Tanagers (Thraupinae) and finches (Emberizinae) «masticate» fruit and discard the seeds before ingesting the pulp (Levey 1986). By eluding the filling of the digestive tract with indigestible ballast,

they ameliorate the constraints of limited gut capacity (Levey and Grajal 1991, Martínez del Rio and Restrepo 1993). Interestingly, no tanager or emberizid finch is known to lek. The only frugivores that lek swallow seeds whole. The tropical fruits eaten by lekking frugivores vary widely in their pulp composition. Not all of them can be considered energy-dilute and bulky. For instance. lekking cotingas (Cotingidae) and Birds of Paradise (Paradisaeidae) feed on lipid and energy rich fruits (Snow 1976, Beehler 1983, 1989). These birds might in turn, be constrained by the slow digestion of complex lipid molecules and, might require different digestive adaptations than birds that feed on dilute, carbohydrate rich fruits (Bosque and Parra 1992, Place and Stiles 1992, Fuentes 1994). Understanding constraints imposed by processing such fruits might help to further understand the variety of mating adaptations within frugivores (e.g. Beehler 1983, 1989, Beehler and Pruett-Jones 1983, Diamond 1986). Likewise, not all foliage eaters extensively ferment plant constituents as do grouse. Among the Anatidae (ducks and geese), some foliage eating taxa have a contrasting digestive strategy to that of grouse. Foliage-eating geese and ducks have relatively fast gastrointestinal turnover rates and therefore low digestion of cell wall polysaccarides and low overall digestibility of organic matter (Buchsbaum, et al 1986, Dawsonm et al 1989, Prop and Vulink 1992), since the efficiency of digestion by herbivores is closely related to retention time of the food (Sibly 1981, Demment and Van Soest 1985). Consequently, to meet their energy requirements, large amounts of food must be consumed and since geese are highly selective feeders (Owen 1972, Sedinger and Raveling 1984) and have relatively large body masses, they must spend as much as 90% of their daylight hours in feeding, especially in autumn and winter when days are shorter (Owen 1972, Prop and Vulink 1992) and pairing frequently occurs among the Anatidae (Johnsgard 1965). Under such time constraint it is then not surprising that no geese or duck is known to lek (Payne 1984, Johnsgard 1994). Hence to improve our understanding of how lekking behavior

in birds is related to a vegetable diet, we should also consider the varied digestive adaptations of the birds to such diets.

A digestive bottle-neck (Kenward and Sibly 1977) is not a sufficient condition for the evolution of lekking behavior, just as emancipation of the male from parental duties is not. Thus in Wood Pigeons (*Columba palumbus*) food intake is limited by the rate at which gut volume becomes available for more food (Kenward and Sibly 1977), but they do not form leks. The limitation of energy intake by digestive processes might facilitate the evolution of lekking behavior in birds; it might even be a necessary pre-condition; but it is clearly not a sufficient condition.

In addition to examples discussed above lekking is also known in a few other groups of birds: e.g. among calidrine sandpipers (Scolopacidae), African honey-guides (Indicatoridae) and Bustards (Otididae) (Payne 1984, Johnsgard 1994). Note that digestive bottle-necks have been shown to occur under natural conditions in two species of scolopacids, the Sanderling (*Callidris alba*) and the Whimbrel (*Numenius phaeopus*) (Castro, et al 1989, Zwarts and Dirksen 1990). Likewise, in honey-guides' digestion might be a complex process enhanced by symbiotic microorganisms (Friedmann and Kern 1956, but see Diamond and Place 1988). Digestive physiology of Bustards is not known. More generally it might be significant that virtually all species of mammals that lek are fiber digesters (ruminant artiodactyls) or frugivores (Bradbury 1977, Krebs and Davies 1993).

The effect of phylogeny

It is currently recognized that the effects of common ancestry must be considered when examining questions about adaptation in comparative studies (e.g. Harvey and Pagel 1991). Therefore, it would be necessary to determine if correlations described in this note could simply be due to common evolution within taxa rather than to common diet and its processing consequences. A detailed analysis of this problem is beyond the

purpose of this note, but Höglund's (1989) phylogenetic analysis of lekking behavior in birds (in relation to sexual dimorphism), provides a preliminary answer. Höglund concludes that lekking has evolved independently in 11 families of birds, and that within most of them lekking evolved in several independent instances. The most parsimonious solutions of the phylogenies show that lekking has evolved three times among Tetraonidae, twice among Scolopacidae, three times in Cotingidae, three times in Pipridae, probably two or three times in Trochilidae, twice among Ploecidae (following Höglund's classification of leks), in addition to those instances in several other families in which only one genus exhibits lek breeding and it can be safely assumed that in them, the evolution of lekking was an independent evolutionary event. Therefore, it would not be correct to assume that lekking is, for instance, common among cotingas simply because of common evolution, since lekking has evolved a minimum of three times in this group. Furthermore, Höglund's analysis demonstrates that sharing of lekking behavior by phylogenetically related families needs not to be simply the result of common ancestry. For instance, since Pipridae (manakins) and Cotingidae are sister taxa (Lanyon 1985), it would be tempting to think that lekking is common to both families because of common ancestry. That this is not the case can be inferred from Höglund's results that show that non-lekking is the ancestral state in the phylogenies of both groups. Therefore lekking evolved independently in each of them. A similar argument could be made regarding phylogenetically related Paradisaeidae (birds of paradise) and Ptilonorhynchidae (bowerbirds). What cotingas and manakins and birds of paradise and bowerbirds have in common (in addition to ancestry), is their extensively frugivorous habits.

To conclude: the evolution of leks in birds and other vertebrates might be better understood by considering, in addition to ecological and phylogenetic factors, the constraints and consequences of food processing after ingestion.

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