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Allocation of reproductive effort by breeding Blackbirds, family Icteridae

Asignación de esfuerzo reproductivo en aves de la familia Icteridae

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ABSTRACT

Because breeding activities, such as courtship feeding, nest building, incubation, advertising for mates, feeding young and defending territories, compete for available time, patterns of investment in these activities can reveal important aspects of the evolution of reproductive behavior. This survey of parental investment patterns in the avian family Icteridae, reveals that some patterns are highly conservative in the family while others are variable. Among the conservative traits are that females of every species build nests, incubate eggs and feed nestlings and fledglings, and that males apparently never incubate and rarely build nests. Feeding of the incubating female by the male is also very rare in the family. Among monogamous species both sexes feed nestlings and fledglings but males generally feed less than their mates. Males of polygynous species may or may not feed nestlings and there may be considerable intraspecific geographical variation in this behavior. These patterns might be explained by assuming that the patterns observed are those that yield the highest fitnesses to the individuals.

Alternatively, some of these behaviors may benefit one sex but be detrimental to the other. Evolutionary stabilization in such cases could be achieved if it were difficult for individuals of one sex to predict the behavior of potential spouses, and if terminating the bond once the behavior is known is more disadvantageous than remaining in it. Finally, some aspects of the patterns may reflect evolutionary conservatism within taxonomic lineages. Each of the parental investment patterns is discussed in this context, and ways of distinguishing among the hypotheses are proposed.

Key words: Reproductive tactics, parental investment patterns, social systems, adaptation models, blackbirds, Icteridae.

RESUMEN

Debido a que las actividades reproductivas, tales como alimentación de la pareja durante el cortejo, construcción del nido, incubación, atracción de parejas, alimentación de los pichones y defensa de territorios, compiten por el tiempo disponible, los patrones de inversión en estas actividades pueden revelar aspectos importantes acerca de la evolución del comportamiento reproductivo. Esta revisión de los patrones de asignación de esfuerzo reproductivo en aves de la familia Icteridae revela que algunos patrones son marcadamente conservativos en la familia mientras que otros son variables. Entre los rasgos conservativos se encuentra el que las hembras de todas las especies construyen los nidos, incuban los huevos y alimentan a los pichones en el nido y después de salir de éste, y que los machos aparentemente nunca incuban y rara vez construyen los nidos. En esta familia también es muy raro que los machos alimenten a las hembras mientras ellas incuban. En las especies monógamas los individuos de ambos sexos alimentan a los pichones en el nido y fuera de éste, pero los machos generalmente lo hacen menos que las hembras. Los machos de las especies polígamas pueden o no alimentar a los pichones en el nido, y una considerable variación geográfica intraespecífica puede existir en este comportamiento. Estos patrones pueden ser interpretados suponiendo que aquellos observados son los que proveen las mayores adecuaciones biológicas (fitnesses) a los individuos.

Alternativamente, algunos de estos comportamientos pueden beneficiar a un sexo y ser perjudiciales al otro. En tales casos, la estabilidad evolutiva pudiera alcanzarse si fuese difícil para los individuos de un sexo predecir el comportamiento de su posible pareja, y si el abandonar el vínculo una vez que el comportamiento es conocido es más desventajoso que el mantenerlo. Finalmente, algunos aspectos de los patrones discernidos pueden reflejar un conservantismo evolutivo. Cada uno de los rasgos es discutido dentro de este contexto y se proponen maneras de distinguir entre las diferentes hipótesis.

Palabras claves: Tácticas reproductivas, patrones de inversión parental, sistemas sociales, modelos de adaptación, aves Ictéridas.

INTRODUCTION

Patterns of allocation of time to various activities, such as courtship feeding, incubation, advertising for additional mates, feeding young and defending territory, are basic components of avian social system. Because all of these activities

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could be performed better if more time could be allocated to them, allocation patterns are likely to affect reproductive success. Due to differences in their energy commitment to gamete production, males and females usually receive different benefits from their time allocations (Trivers 1972). Males produce energetically inexpensive gametes and can usually enhance their reproductive success by inseminating as many females as possible, whether or not they help rear the offspring they have sired. Females, on the other hand, produce gametes with high energy contents. The number of offspring they can produce is usually limited by the amount of energy that can be allocated to egg production and subsequent offspring care and not by the number of males with which the female is able to mate. Birds are excellent subjects for the study of time allocation patterns because their eggs and sperm are markedly different in size, and because, other than gamete production, males and females may be assumed to be capable of performing all reproductive activities with approximately equal ease. Therefore, differences between male and females allocation patterns should reflect differences in the benefits resulting from these allocations rather than being byproducts of stringent physiological limitations such as characterize mammals, where nutrition of offspring inevitably falls primarily on females.

A comparative examination of reproductive effort within and between pair bonds can also provide insights into possible constraints on the ways in which organisms adapt to their environments. Much of recent theory in behavioral ecology is developed by posing some problem and then devising behavioral rules which, if followed, should increase survivorship and reproductive success over what they would be if other behavioral rules were followed. An implicit assumption is that if particular behavioral patterns are appropriate, they will evolve rapidly enough so that most organisms should employ the "best" patterns. Considerable success has been achieved with the development and testing of theories of this type, most notably in the area of foraging theory (Cowie 1977, Krebs *et al.* 1978, Kramer & Nowell 1980, Orians & Pearson 1979, Pyke *et al.* 1977, Stephens & Charnov 1982), but also in areas of mate selection theory (Crook 1962, 1964, Orians 1969, Searcy 1982) and habitat selection theory (Hilden 1965, Levins 1968, Orians 1980, Partridge 1978, Rosenzweig 1974, 1981).

Success with these models is due in part to the fact that the theories do not ask organisms to perform radically new or different behaviors. All that is required is that the animal be capable of altering its decisions from among those organisms or sites already recognized as prey, potential mates, or settling places. These models also operate within the constraints imposed by existing morphological traits of the animals in question. However, many problems in adaptation are not of this type. In many cases, appropriate responses by the animal may require a new behavior pattern which, in turn, requires new neural circuitry. Many aspects of reproductive activities, such as incubation, feeding of offspring, and building of nests, probably fall into this category. Development of incubation behavior by members of a sex that has previously not incubated may not be as difficult as development of functional mammary glands among male mammals. But we should not assume that such changes, because they involve primarily altered neural circuitry rather than evolution of external morphological structures, will necessarily arise and be incorporated rapidly into the behavioral repertories of animals just because that would be advantageous.

In all cases, however, it is important to develop "perfect adaptation models" which assume that no significant evolutionary constraints are operating. Without such models there is no basis for assessing whether a pattern of behavior is "suboptimal" under current circumstances. The "no constraint models" function as evolutionary null models against which real behavior can be compared to determine whether or not there really are significant anomalies that require explanation. Extensive knowledge of relevant natural history is very helpful in erecting and evaluating behavioral ecological models. Indeed, models of foraging theory owe their success in part to the fact that they were produced by people with extensive natural history knowledge which they used creatively in developing the models and orienting them toward problems faced by real animals.

The study of patterns of behavior among

a variety of organisms is often helpful in revealing nonobvious patterns and identifying which patterns are highly variable and which are relatively constant within and between groups. Traits that differ strikingly among closely related species are ones that can and do evolve rapidly. Constancy can mean either that the particular pattern is a robust solution to some important problem in a wide variety of circumstances or that the traits in question are, for other reasons, constrained in their ability to evolve in response to selective pressures. Therefore, although identification of patterns among species does not immediately provide answers to their causation, it does serve to identify those patterns that are of great interest and worthy of especially serious attention.

In this paper, I explore some patterns of reproductive behavior among the American blackbirds, family Icteridae. This distinctive group of birds includes about 94 species confined to the New World. As breeding birds, they range from Alaska and northern Canada to Tierra del Fuego, and they occur in most of the habitat types found in both continents. They have been extensively studied because they are often common and conspicuous, because many of them nest in open country where they are easily observed, and because of the rich variety of their social systems (Orians 1972). Among the icterids are monogamous, polygynous and promiscuous species, the non-monogamous species being found primarily among marsh-nesting insectivores and tropical frugivores (Table 1). There are also territorial and colonial species, with coloniality being well developed among species of forests, savannahs and marshes (Table 2). There is no overall association between sexual size dimorphism and plumage dimorphism because the sexes of migratory, monogamous species are similar in size but not in plumage, while many tropical, colonial species are highly sexually dimorphic in size but not in plumage (Lowther 1975). There is, however, more plumage dimorphism at higher latitudes than in tropical regions, and plumage dimorphism is especially prominent among marsh-nesting species. Sexual dimorphism in size is strongly correlated with non-monogamous mating systems (Lowther 1975, Selander 1972).

Patterns of Reproductive Effort

The basic outlines of breeding social organization are known for enough species of icterids that the patterns suggested by existing data are not likely to be seriously altered by future studies. Despite the great variations in social organization and ecology within the family, some aspects of reproductive effort are constant in all species. Most species are alike for some other patterns, while some behaviors are highly variable both within and among species.

The most constant reproductive behavior patterns among icterids are that females in every species build nests, incubate eggs, and feed nestlings and fledglings. In contrast, incubation by males is virtually absent in the family. Grimes (1931) reported incubation by male Orchard Orioles (*Icterus spurius*) but subsequent studies of this species have not reported other instances of that behavior (Bent 1958). A number of sexually monomorphic species have been examined closely enough to assure that male incubation in these species has not been overlooked because of the difficulties of sexing individuals. Moreover, no males have been reported to assume incubation duties when their mates have been lost.

Feeding of the incubating female is also very rare among icterids. Skutch (1954) reported feeding of the incubating female by the male Melodius Blackbird (*Dives dives*) but Orians (1983) did not observe it at a nest under careful observation. The incubating female Rusty Blackbird (*Euphagus carolinus*) is sometimes fed by the male although data on the frequency with which this is done have not been published (Kennard 1920, Nero 1984).

In nearly every species of icterid, nests are built entirely by the female. Males of many monogamous species accompany their mates to and from nests under construction but without making any contribution to the building effort. The only species in which nests are known to be built primarily by the male is the South American Yellow-hooded Blackbird (*Agelaius icterocephalus*) (Wiley & Wiley 1980). In Argentina I observed a male Chestnut-capped Blackbird *(Agelaius ruficapillus)* building a nest while his mate incubated eggs at another, but whether

TABLE 1

Habitat, diet and paring patterns among the icterids

Hábitat, dieta y patrones de apareamiento en aves ictéridas

HABITAT	DIET	MONOGAMOUS	POLYGYNOUS	FAMILY GROUPS	REFERENCES
Forests	Insectivorous	*Nesopsar nigerrimus*			Cruz (1978)
		Cacicus holosericeus			Skutch (1954)
		C. uropygialis			Orians (unpublished)
		C. solitarius			Naumberg (1930)
Forests	Frugivorous		*Psarocolius montezuma*		Skutch (1954)
			P. wagleri		Chapman (1928)
			P. decumanus		Tashian (1957)
			P. angustifrons		Drury (1962)
			Cacicus cela		Skutch (1954), Feekes (1981)
			C. haemorrhous		Drury (1962), Feekes (1981)
Savannahs	Insectivorous	*Dives dives*			Skutch (1954), Orians (1983)
				Curaeus curaeus	Orians, Orians & Orians (1977)
		Euphagus cyanocephalus			Horn (1968), Williams (1952)
		Icterus (most species)			Bent (1968) and others
		Agelaius xanthomus			Post & Wiley (1976, 1977)
		Quiscalus quiscula			Bent (1955), Ficken (1963)
		Q. niger			Orians (unplublished)
Grasslands	Insectivorous		*Dolichonyx oryzivorus*		Kendeigh (1941), Martín (1974), Wittenberger (1980)
		Sturnella magna – – – – – – –	– – – – – →		Lanyon (1957)
		S. neglecta – – – – – – – – –	– – – – – →		Lanyon (1957)
		Leistes militaris			Hudson (1923)
		Pezites militaris			Short (1968)
		P. defilippi			Short (1968)
		Molothrus ater			Bent (1958), Darley (1982)
		M. bonariensis			Wetmore (1926), Fraga (in prep)
				Molothrus badius	Fraga (in prep), Orians *et al.* (1977)
		M. rufoaxillaris			Fraga (in prep), Hudson (1923)
Deserts	Insectivorous			*Oreopsar bolivianus*	Orians, Erckmann & Schultz (1977)
				Dives warczewiczii	Orians (1983)
		Icterus nigrogularis			Bosque (pers. comm.)
Bogs	Insectivorous	*Euphagus carolinus*			Bent (1958)
Marshes	Insectivorous		*Xanthocephalus xanthocephalus*		Willson (1966)
			Agelaius tricolor		Bent (1958), Orians (1972)
			A. phoeniceus		Bent (1958), Orians (1972)
		Agelaius thilius			Orians (1980)
		A. icterocephalus			Wiley & Wiley (1980)
		A. xanthopthalmus			Short (1968), Terborgh (pers. comm.)
		Pseudoleistes virescens			Hudson (1923), Orians *et al.* (1977)
		Amblyramphus holosericeus			Orians (1980)
			Quiscalus major		Selander & Giller (1961)
			Q. mexicanus		Selander & Giller (1961)

TABLE 2

Association between grouping patterns and habitat among icterids.

Asociación entre patrón de agrupamiento y hábitat en aves ictéridas

HABITAT	TERRITORIAL	GROUPED TERRITORIES	COLONIAL	REFERENCES
Forests	*Nesopsar nigerrimus*			Cruz (1978)
	Cacicus holosericeus			Skutch (1954)
	C. solitarius			Naumberg (1930)
			Psarocolius montezuma	Skutch (1954)
			P. wagleri	Chapman (1928)
			P. decumanus	Tashian (1957)
			Cacicus cela	Feekes (1981), Skutch (1954)
			C. haemorrhous	Feekes (1981)
			C. melanicterus	Orians (unpublished)
Savannahs	*Dives dives*			Skutch (1954)
	Icterus (most species)			Bent (1958) and others
			Euphagus cyanocephalus	Horn (1968), Williams (1952)
			Agelaius xanthomus	Post & Wiley (1976, 1977)
			Quiscalus quiscula	Bent (1958), Ficken (1963)
			Q. niger	Orians (unpublished)
Grasslands	*Dolichonyx oryzivorus*			Kendeigh (1941), Martin (1974), Wittenberger (1980)
	Sturnella magna			Lanyon (1957)
	Sturnella neglecta			Lanyon (1957)
	Leistes militaris			Hudson (1923)
	Pezites defilippii			Short (1968)
	P. militaris			Short (1968)
	Molothrus ater			Bent (1958), Darley (1982)
Deserts	*Icterus nigrogularis*			Bosque (pers. comm.)
	Oreopsar bolivianus			Orians, Erckmann & Schultz (1977)
Marshes		*Xanthocephalus xanthocephalus*		Willson (1966)
		Agelaius phoeniceus		Bent (1958), Orians (1972)
		A. icterocephalus		Wiley & Wiley (1980)
		A. ruficapillus		Orians (unpublished)
			Agelaius tricolor	Orians (1961)
			A. thilius	Orians (1980)
			Pseudoleistes virescens	Orians *et al.* (1977)
			Quiscalus major	Selander & Giller (1961)
			Quiscalus mexicanus	Selander & Giller (1961)
			Q. nicaraguensis	Orians (unpublished)
	Amblyramphus holosericeus			Orians (1980)
Bogs		*Euphagus carolinus*		Bent (1958)

this was standard or unusual behavior is not yet known. Male and female Melodious Blackbirds of Central America share in building the nest (Skutch 1954). There are sporadic reports of nest building by male Hooded Orioles (*Icterus cucculatus*), Orchard Orioles (*I. spurius*), and Baltimore Orioles (*I. galbula*) (Bendire 1895, Dawson 1923, Nuttall 1932), but since males of many monogamous species pick up nesting material but drop it without actually incorporating it in a nest, care is needed in making and interpreting observations. The rarity of nest building by male icterids is surprising because in the ecologically and socially similar weaver birds (*Ploceidae*), males are the primary nest-builders in many species (Brosset 1978, Crook 1962, 1963, 1964, Collias & Collias 1964, 1967).

Male contribution to feeding of nestlings and fledglings is highly variable among icterids. In all monogamous species, both sexes feed nestlings and fledglings, but males generally feed less often than their mates. Among polygynous species, males may or may not feed nestlings and fledglings (Table 3). Males are not known to bring food to their offspring in any of the polygynous tropical frugivores. Among marsh —and grassland— nesting polygynous species, the roles of males are highly variable, both within and between species. Male Red-winged Blackbirds (*Agelaius phoeniceus*) usually do not feed nestlings but they do normally feed fledglings. There is geographic variability in this behavior, however. In Indiana, about half of the males in a breeding population fed nestlings, and the probability that a male fed nestlings increased with his age (Yasukawa 1977, Patterson 1979). In Washington State, male Redwings, regardless of their age, seldom feed nestlings, but they do regularly feed fledglings. Male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) usually feed nestlings, concentrating their effort on the first nest to hatch on their territory (Willson 1966). Male Bobolinks (*Dolichonyx oryzivorus*) feed nestlings, usually at the nest of their first female (Wittenberger 1980).

Male contributions to feeding of offspring have been investigated experimentally and by observing correlations between ecological conditions and male behavior. Preferential feeding of first broods by males of polygynous species is expected because older young have a higher reproductive value than younger nestlings by

TABLE 3

The role of males of polygynous icterids in feeding young

Papel de los machos de aves ictéridas políginas en la alimentación de las crías

GENUS	Known number of polygynous species	NUMBER OF SPECIES IN WHICH: Males feed nestlings	Males don't feed nestlings	Unknown
Oropendolas (*Psarocolius*)	12	1	4	7
Caciques (*Cacicus*)	3	0	3	0
Yellow-headed Blackbird (*Xanthocephalus*)	1	1	0	0
Redwings and allies (*Agelaius*)	3	2	0	1
Meadowlarks* (*Sturnella*)	2	2	0	0
Grackles (*Quiscalus*)	3	0	2	1
Bobolink (*Dolichonyx*)	1	1	0	0
TOTALS	25	7	9	9

* Weakly polygynous.

virtue of having survived more of their highly vulnerable dependency period. However, if the value of food to the nestlings is highly unequal in first and second nests, then males should adjust their feeding accordingly. Differences in value of male feeding can arise for at least two reasons. First, if nestlings in the primary nest are well fed, either because the female is unusually efficient or because foraging conditions have been favorable, but those in a secondary nest are undernourished, then the male can contribute more to his reproductive success by favoring his secondary nest. This is the situation reported among Bobolinks by Wittenberger (1980).

Second, the value of male feeding can vary as a function of the number of young in the nest. The probability of nestling survival is zero below a certain parental feeding effort. Above that effort the chance of survival increases, reaching an asymptote beyond which no further feeding effort makes any difference. At any given level of parental effort, the marginal value of additional effort is given by the slope of the line tangent to the survival curve at that point. The probability that a male feeds at a given nest should be positively correlated with the marginal value of his contribution at that nest (Patterson *et al.* 1980).

This hypothesis was tested by reducing clutches of Yellow-headed Blackbirds from four to two eggs in primary nests on experimental territories while all nests were maintained with full clutches of four eggs on the control territories. Males on all experimental territories switched their feeding to the nests of their secondary females after those nestlings hatched, whereas all control males continued to feed only at their primary nests (Patterson *et al.* 1980). Attempts to induce males to feed at tertiary nests by reducing clutches on both primary and secondary nests were unsuccessful. On these territories, males continued to feed at their primary nests. However, male Yellowheads have subsequently been induced to feed nestlings at tertiary nests (D. Gori, personal communication 5/83).

Whether or not males bring any food to nestlings also can be adjusted to proximate ecological conditions. A male of a polygynous species faces a conflict between investing his time in feeding nestlings, territory defense, and attempting to attract additional mates. These activities are mutually exclusive over short time periods, although a male can perform all of them within a single day. However, if a male, by taking time out to feed nestlings, reduces his chances of attracting additional females, he may lower his overall reproductive success. The value of feeding nestlings depends on the nutritional status of the young when fed by the female alone, on nest predation rates, and on the influence of male activity around the nest on nest predation rates. The value of continuing to attract mates depends on the arrival rate of potential new mates and the influence of male behavior on the probability that females will settle on his territory.

If these general relationships are true several predictions follow. First, males should be less likely to feed nestlings when new females continue to arrive over extended time periods so that high arrival rates coincide with the nestling period. Second, males should be less likely to bring food when the nestlings are being fed adequately by the unaided females. The first of these two conditions is met among breeding Red-winged Blackbirds in Washington State because young females start to nest long after older females do and, because of high nest predation rates, many females change nesting locations following destruction of their first nests. In these populations, males rarely feed nestlings. In the same marshes, nesting of Yellow-headed Blackbirds is much more synchronous. Most females begin nesting, within a two-week period, second broods are not reared, and there is relatively little re-nesting after failure. As expected, male Yellowheads regularly feed nestlings whereas male Redwings do not.

However, these arguments cannot explain the failure of males of the colonial, tropical frugivorous icterids to feed nestlings. In these species, new nests are not added to colonies at the time young are available to be fed in the earliest nests. The males may move to other colonies, but some of them are known to remain near their original nesting colony and function as signallers of the presence of predators and as attackers of predators near the nests (Feekes 1981, 1982). The value of the males as nest defenders may outweigh their value as feeders of nestlings, but there is no direct test available of this postulate.

DISCUSSION

These patterns of parental reproductive investment among icterids can be explained by at least three rather different theoretical arguments. The first suggests that the existing roles of males and females in all species are actually the ones that yield highest fitnesses to those individuals. For purposes of discussion, I will call this the "Perfect Adaptation Model". It argues that male icterids do not, to use incubation and provisioning their mates as an example, incubate or feed incubating females because their own reproductive success is thereby enhanced. The fact that males are usually brighter and more conspicuous than females and might pose greater risks to the nest and its contents by attracting predators if they incubated, supports this interpretation. This is a weak argument, however, because males do not incubate in sexually monomorphic icterids, males *do* incubate in many other passerine birds even when they are brighter than females, and brilliantly colored males regularly feed incubating females in many species in other passerine families (Skutch 1976). No plausible argument has yet been advanced why bright male icterids pose greater risks to their nests than do males of those other species.

Alternatively, it is possible that males, being larger than females in all icterids (Table 4), are better guarders of the nest and territory, and, therefore, breeding success is enhanced by a segregation of roles. This interpretation has been used by Feekes (1981, 1982) to explain the absence of male parental investment in colonial Caciques. Even if correct, however, this argument by itself does not explain the failure of males to take over incubation or nestling feeding when they lose their mates. Only if the expected success of males attempting to rear nestlings unaided is so low that it is better to abandon the nesting attempt entirely should males fail to assume parental duties.

The Perfect Adaptation Model assumes that it is in the best "evolutionary interests"

TABLE 4

Mating systems and size dimorphism among icterids (after Lowther 1975)

Sistemas de apareamiento y dimorfismo sexual en aves ictéridas (según Lowther 1975)

GROUP	Mating patterns	Spacing patterns	Average difference in size between sexes (percent)	Range of size differences (percent)
Oropendolas (*Psarocolius*)	Polygynous	Colonial	25	15-35
Caciques (*Cacicus*)	Polygynous	Colonial	22	21-23
Caciques (*Cacicus*)	Monogamous	Territorial	12	10-15
Orioles (*Icterus*)	Monogamous	Territorial	6	0-14
Oriole Blackbird (*Gymnomystax*)	Monogamous	?	5	
Yellow-headed Blackbird (*Xanthocephalus*)	Polygynous	Territorial	20	
Redwings (*Agelaius*)	Polygynous	Territorial	15	12-18
Other (*Agelaius*).	Monogamous	Varied	7	6-14
Meadowlarks (*Sturnella*)	Monogamous	Territorial	8	5-11
Brown-and-yellow Marshbird (*Pseudoleistes*)	Monogamous	Colonial	5	
Scarlet-headed Blackbird (*Amblyramphus*)	Monogamous	Territorial	6	
Austral Blackbird (*Curaeus*)	Monogamous	Territorial	6	
Melodius Blackbird (*Dives*)	Monogamous	Territorial	10	
Grackles (*Quiscalus*)	Monogamous	Colonial	13	11-14
Grackles (*Quiscalus*)	Polygynous	Colonial	21	20-22
Euphagus	Monogamous	Colonial	7	5- 8
Cowbirds (*Molothrus*)	Monogamous	Varied	9	5-12
Giant Cowbird (*Scaphidura*)	Polygynous	Colonial	24	
Bobolink (*Dolichonyx*)	Polygynous	Territorial	11	

of both males and females for males to refrain from incubating or feeding their incubating spouses. The "Competitive Adaptation Model" states that observed patterns may be advantageous to one sex but not to the other. For example, males might benefit by not incubating or feeding incubating females whereas females would gain if the males did so. Females might be unable to influence male incubation or feeding behavior because (a) they are unable to assess the probability that a male will incubate or provide food at the time pair bonds are formed, and (b) because by the time females discover that their mates will not incubate, they cannot improve their situation by deserting. Moreover, if no males incubate or feed their incubating mates, there is no variability from among which females can choose. Because predicting future behavior of associates is always difficult, females can be in an evolutionary stable "cruel bind". It is noteworthy that incubation and feeding of incubating females by males has not been reported in other closely-related passerine families, such as Parulidae and Thraupidae (Skutch 1976), suggesting that this pattern may be an evolutionarily conservative one.

The third theoretical approach, here called the "Constrained Adaptation Model", argues that patterns of reproductive effort different from those observed might actually be advantageous to individuals of both sexes, but that suitable genetic variation has not been available to produce them. Evolution of incubation by males in a population initially lacking it is a complex evolutionary change. The appropriate breast tissues may not respond properly to hormonal stimulation, and the neural circuitry required to cause males to perform a new behavioral act (incubation) might not readily arise. Icterids may well have arisen from ancestors lacking male incubation, because male incubation is rare among the Emberizidae, the presumed ancestral family to the Icteridae (Skutch 1976).

Similar arguments could be advanced in the case of the more variable traits, such as male feeding of nestlings. Even though experimental and observational studies have demonstrated considerable flexibility in these behaviors within a species, it is nonetheless possible that the lack of feeding of nestlings by male Caciques and Oropendolas could be due to a failure of the appropriate behavorial components to arise. Nonetheless, this form of argument is weaker for variable traits than it is for ones that appear to be fixed or nearly so within the family.

The evolution of responses to avian brood parasitism may also be similarly constrained. With the single exception of Smith's (1968) study of parasitism by Giant Cowbirds (*Scaphidura oryzivora*) on Oropendolas in Panamá, every study has shown that nests parasitized by Cowbirds (also in the family Icteridae) produce fewer young than unparasitized nests (Friedmann *et al.* 1977, Klass 1975). The evolution of rejection behavior depends not only on the physical ability of the victim to remove the parasite's egg, but on the development of behavior patterns very different from those normally shown towards eggs in one's nest. A rejector must be able to discriminate the parasite's egg from its own and to pick up an egg from its own nest and throw it out, an act that is, under normal circumstances, highly unadaptive. There are reasons to believe that this is not easily accomplished even though rejection spreads rapidly through a population once it arises (Rothstein 1975, 1976). At least some cases of failure to evolve rejection may be due to the inability of small hosts to remove eggs of the parasite (Rohwer, in prep.), but others may represent suboptimal behavior.

The varied activities performed by parent birds during the breeding season not only compete for time, but they also are qualitatively very different. We know relatively little about the organization of the avian brain and how the capacity to perform such activities is programmed and coordinated. Nonetheless, the development of complex behaviors may require long periods of evolutionary time. At any given moment in time, species may lack the ability to behave in ways that would actually be advantageous to the component individuals. In this general sense, the Constrained Adaptation Model is inevitably true. The challenge, however, is to determine which patterns are really best explained by assuming evolutionary constraints and which really represent finely-tuned adaptations.

The traits in which the icterids are quite constant, namely who builds the nest, who incubates, and whether or not the male feeds the incubating female, are all ones in which acquisition of the behavior on the part of the male is a nontrivial innovation. Other constant traits, such as feeding of nestlings by both sexes in all monogamous species, could reflect a uniform advantage, either inherited from emberizid ancestors or acquired sufficiently long ago that all species now have it. Variable traits, such as whether or not the male of polygynous species feeds nestlings and, if so, how his efforts are allocated, are consistent with the notion of fine tuning of a response which requires primarily adjustment of toward whom the behavior is directed. Lack of feeding by males of many of the polygynous species, particularly Oropendolas and Caciques, however, remains a puzzle.

Further elucidation of the meanings of these patterns will require both experimental analyses of variable traits and seeking of still broader patterns of reproductive behavior of passerine birds in the light of the improved phylogenies that are becoming available as a result of new techniques of assessing evolutionary relationships (Sibley & Ahlquist 1983). The comparative approach which has played such an important role in the analysis of the forms of communicative displays, has an equally promising role to play in the study of patterns of reproductive behavior among birds and other animals.

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LITERATURE CITED

BENDIRE CA (1895) Life histories of North American birds. United States National Museum Special Bulletin 3.

BENT AC (1958) Life histories of North American blackbirds, orioles, tanagers, and allies. United States National Museum Bulletin 211.

BROSSET A (1978) Social organization and nest-building in the forest weaver birds of the genus *Malimbus* (Ploceinae). Ibis 120: 27-37.

CHAPMAN FM (1928) The nesting habits of Wagler's Oropendola (*Zarhynchus wagleri*) on Barro Colorado Island. Bulletin of the American Museum of Natural History 58: 123-166.

COLLIAS NE & EC COLLIAS (1964) Evolution of nest-building in the weaverbirds (*Ploceidae*). University of California Publications in Zoology 73: 1-239.

COLLIAS NE & EC COLLIAS (1977) Weaverbird nest aggregation and evolution of the compound nest. Auk 94: 50-64.

COWIE RJ (1977) Optimal foraging in Great Tits, *Parus major.* Nature, London 268: 137-139.

CROOK JH (1962) The adaptative significance of pair formation types in weaver birds. Symposium Zoological Society of London 8: 57-70.

CROOK JH (1964) The evolution of social organization and visual communication in the weaver birds (Ploceinae). Behavior Supplement 10.

CRUZ A (1978) Adaptive evolution in the Jamaican Blackbird *Nesopsar nigerrimus.* Ornis Scandinavica 9: 130-137.

DARLEY JA (1982) Territoriality and mating behavior of the male Brown-headed Cowbird. Condor 84: 15-21.

DAWSON WL (1923) The birds of California. Volume 1, South Moulton Company, San Francisco, California.

DRURY WJ Jr. (1962) Breeding activities, especially nest building of the Yellowtail (*Ostinops decumanus*) in Trinidad, West Indies. Zoologica 47: 39-58.

FEEKES F (1981) Biology and colonial organization of two sympatric caciques, *Cacicus c. cela* and *Cacicus h. haemorrhous* (Icteridae: Aves) in Surinam. Ardea 69: 83-107.

FEEKES F (1982) Song mimesis within colonies of *Cacicus c. cela* (Icteridae: Aves). A colonial password? Zeitschrift für Tierpsychologie. 58: 119-152.

FICKEN RW (1963) Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula.* Auk 80: 52-72.

FRIEDMANN H, LF KIFF & SI ROTHSTEIN (1977) A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions to Zoology 235: 1-75.

GRIMES SA (1931) Notes on the Orchard Oriole. Florida Naturalist 5: 1-7.

HILDEN O (1965) Habitat selection in birds. Annales Zoologici Fennici 2: 53-75.

HORN HS (1968) The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). Ecology 49: 682-694.

HUDSON WH (1923) Birds of La Plata. J. M. Dent & Sons, London.

KENDEIGH SC (1941) Birds of a prairie community. Condor 43: 165-174.

KENNARD FH (1920) Notes on the breeding habits of the Rusty Blackbird in northern New England. Auk 37: 412-422.

KLASS EE (1975) Cowbird parasitism and nesting success in the Eastern Phoebe. Occasional Papers, Museum of Natural History, University of Kansas 41: 1-18.

KREBS JR, A KACELNIK & P TAYLOR (1978) Tests of optimal sampling by foraging Great Tits. Nature 275: 27-31.

KRAMER DL & W NOWELL (1980) Central place foraging in the Eastern Chipmunk *Tamias striatus.* Animal Behavior 28: 772-778.

LANYON WE (1957) The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publication Nuttall Ornithology Club 1: 1-67.

LEVINS R (1968) Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

LOWTHER PE (1975) Geographic and ecological variation in the family Icteridae. Wilson Bulletin 87: 481-495.

MARTIN SG (1974) Adaptations for polygynous breedin in the Bobolink, *Dolichonyx oryzivorus.* American Zoologist 14: 109-119.

NAUMBERG EMB (1930) The birds of Matto Grosso, Brazil. Bulletin of the American Museum of Natural History 103: 589-603.

NERO RW (1984) Redwings. Smithsonian Institution Press, Washington, D.C.

NUTTALL T (1832) A manual of ornithology of the United States and Canada. Cambridge, Massachusetts.

ORIANS GH (1961) The ecology of blackbird (*Agelaius*) social systems. Ecological Monographs 31: 285-312.

ORIANS GH (1969) On the evolution of mating systems in birds and mammals. American Naturalist 103: 589-603.

ORIANS GH (1972) The adaptive significance of mating systems in the Icteridae. Proceedings XV International Ornithological Congress 1972: 389-398.

ORIANS GH (1980) Habitat selection: general theory and applications to human behavior. In: Lockard J (ed) Evolution of human social behavior. Elsevier, New York: 49-66.

ORIANS GH (1980) Some adaptations of marsh-nesting blackbirds. Princeton University Press, Princeton, New Yersey.

ORIANS GH (1983) Notes on the behavior of the Melodius Blackbird (*Dives dives*). Condor 85: 453-460.

ORIANS GH, L ERCKMANN & JC SCHULTZ (1977) Nesting and other habits of the Bolivian Blackbird (*Oreopsar bolivianus*). Condor 79: 250-256.

ORIANS GH, CE ORIANS & KJ ORIANS (1977) Helpers at the nest in some Argentine blackbirds. In: Stonehouse B & C Perrins (eds) Evolutionary ecology. Macmillan, London: 137-151.

ORIANS GH & NP PEARSON (1979) On the theory of central place foraging. In: Horn DJ, RJ Mitchell & RG Stairs (eds) Analysis of ecological systems. Ohio State University Press, Columbus, Ohio: 155-177.

PARTRIDGE L (1978) Habitat selection. In: Krebs JR & NB Davies (eds) Behavioural ecology: an evolutionary approach. Sinauer Associates, Sunderland, Massachusetts: 351-376.

PATTERSON CB (1979) Relative parental investment in the Red-winged Blackbird. PhD Thesis, Indiana University, Bloomington, Indiana.

PATTERSON CB, WJ ERCKMANN & GH ORIANS (1980) An experimental study of parental investment and polygyny in male blackbirds. American Naturalist 116: 757-769.

POST W & JW WILEY (1976) The Yellow-shouldered Blackbird– present and future. American Birds 30: 13-20.

POST W & JW WILEY (1977) Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79: 176-184.

PYKE GH, HR PULLIAM & EL CHARNOV (1977) Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52: 137-154.

ROSENZWEIG ML (1974) On the evolution of habitat selection. In: Proceedings of the First International Congress of Ecology, Wageningen: 401-404.

ROSENZWEIG ML (1981) A theory of habitat selection. Ecology 62: 327-335.

ROTHSTEIN SI (1975) Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 119: 161-176.

ROTHSTEIN SI (1976) Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93: 498-509.

SEARCY WA (1982) The evolutionary effects of mate selection. Annual Review of Ecology & Systematics 13: 57-85.

SELANDER RK (1972) Sexual selection and dimorphism in birds. In: Campbell B (ed) Sexual selection and the descent of man. Aldine, Chicago, Illinois: 180-230.

SELANDER RK & DR GILLER (1961) Analysis of sympatry of Great-tailed and Boat-tailed Grackles. Condor 63: 29-68.

SHORT LR (1968) Sympatry of Red-breasted Meadowlarks in Argentina and the taxonomy of meadowlarks (Aves: *Leites, Pezites,* and *Sturnella*). American Museum Novitates 2349: 1-30.

SIBLEY CG & JT AHLQUIST (1983) Phylogeny and classification of birds based on the data of DNA-DNA hybridization. In: Johnston RF (ed) Current ornithology 1: 245-292.

SKUTCH AF (1954) Life histories of Central American birds. Pacific Coast Avifauna 31.

SKUTCH AF (1976) Parent birds and their young. University of Texas Press, Austin, Texas.

SMITH NG (1968) The advantage of being parasitized. Nature 219: 690-694.

SMITH W (1947) Orchard Orioles. Migrant 9: 8-16.

STEPHENS DW & EL CHARNOW (1982) Optimal foraging: some simple stochastic models. Behavioral Ecology and Sociobiology 10: 251-263.

TASHIAN RE (1957) Nesting behavior of the Crested Oropendola (*Psarocolius decumanus*) in northern Trinidad, B.W.I. Zoologica 42: 87-97.

TRIVERS RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of Man. Aldine, Chicago, Illinois: 139-179.

WETMORE A (1926) Observations on the birds of Argentina, Paraguay, Uruguay and Chile. United States National Museum Bulletin 133: 1-448.

WILEY RH & MS WILEY (1980) Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. Ecological Monographs 50: 153-178.

WILLIAMS L (1952) Breeding behavior of the Brewer Blackbird. Condor 54: 3-47.

WILLSON MF (1966) Breeding ecology of the Yellow-headed Blackbird. Ecological Monographs 36: 51-77.

WITTENBERGER JF (1980) Feeding of secondary nestlings by polygynous male bobolinks in Oregon. Wilson Bulletin 92: 330-340.

YASUKAWA K 1977) Male quality in the Red-winged Blackbird *(Agelaius phoeniceus).* PhD Dissertation, Indiana University, Bloomington, Indiana.