The Auk 116(1):5–19, 1999

EVOLUTION OF POLYGYNY IN THE ANCESTORS OF RED-WINGED BLACKBIRDS

WILLIAM A. SEARCY,[1,4] KEN YASUKAWA,[2] AND SCOTT LANYON[3]
[1]*Department of Biology, University of Miami, Coral Gables, Florida 33124, USA;*
[2]*Department of Biology, Beloit College, Beloit, Wisconsin 53511, USA; and*
[3]*Bell Museum of Natural History, University of Minnesota, St. Paul, Minnesota 55108, USA*

ABSTRACT.—We map behavioral characters related to mating system onto a phylogeny of the New World blackbirds (family Icteridae) in order to test hypotheses on the evolution of polygyny in Red-winged Blackbirds (*Agelaius phoeniceus*). The two hypotheses we test are "long-term models" in the sense that, unlike most polygyny hypotheses, they allow the ancestral mating system to differ from the present one in characters other than female preferences for mated versus unmated males. In one model, polygyny evolves from the typical territorial monogamy system of most terrestrial passerines; in the second model, polygyny evolves from a system resembling that of monogamous *Agelaius* species, with marsh breeding and without male territoriality. Both hypotheses assume that female-biased parental care coevolves with polygyny. Our reconstruction suggests that the closest non-polygynous ancestor of Red-winged Blackbirds was characterized by monogamy, male territoriality, equal sharing of parental care between the sexes, and terrestrial breeding. Further, polygyny and female-biased care are suggested to have evolved on the same branch as marsh nesting. These results refute our second hypothesis in which polygyny evolves from "*Agelaius* monogamy," while providing provisional support for the first model in which polygyny evolves from territorial monogamy. *Received 27 March 1998, accepted 17 June 1998.*

THE EVOLUTION OF POLYGYNY in birds has been a particular focus of mating-systems research. Hypotheses emerging from work on avian polygyny have been extended both to other taxa and to other mating systems. Polygyny is defined in the ornithological literature as a mating system in which one male forms long-lasting breeding associations with more than one female at a time (Wittenberger 1981). Polygyny hypotheses attempt to explain why a female would mate with a male that is already mated. Existing polygyny models thus concentrate to a large extent on the evolution of a single characteristic, female preference for mated versus unmated males, and assume that other characteristics form a fixed background against which this one trait evolves. We have argued in favor of extending such hypotheses to take a longer view of the evolution of polygyny, beginning with an ancestral mating system that may differ from the present one in many attributes in addition to female preferences (Searcy and Yasukawa 1989, 1995). We have proposed two such long-term models to explain the evolution of polygyny in Red-winged Blackbirds (*Agelaius phoeniceus;* Searcy and Yasukawa 1995). Here, we attempt to test these two models using comparative data on Red-winged Blackbirds and their relatives, the New World blackbirds of the family Icteridae.

Red-winged Blackbirds provide a classic example of territorial polygyny. Males establish territories prior to the nesting season, and females subsequently settle on the territories to breed. In all populations studied, most of the territorial males attract more than one female (Searcy and Yasukawa 1995, Beletsky 1996). The number of young fledged per territory increases with increasing harem size (Beletsky 1996), and a male sires from two-thirds to three-quarters of the young hatched on his territory (Gibbs et al. 1990, Westneat 1993, Weatherhead and Boag 1995, Gray 1996). In such a system, polygyny is of obvious advantage to males, but the reason that females consent to polygynous mating is less obvious, which is why theory has focused on this question. The classic polygyny hypothesis, the polygyny threshold model (Verner and Willson 1966), proposes that polygynous mating is costly to females because a female choosing an already-mated male must share his contribution to parental care and his territorial resources with his previous mates. Choice of an already-mated

---

[4] E-mail: wsearcy@miami.edu

male can nevertheless be advantageous if the female is compensated for the cost of polygyny by obtaining a better territory for nesting (Verner 1964, Orians 1969). By contrast, the neutral mate-choice model and other no-cost hypotheses assume there is no cost of polygyny, so compensation is unnecessary (Lightbody and Weatherhead 1988, Searcy and Yasukawa 1989). Yet other polygyny models assume that there is a cost of polygyny for which females are not compensated, so those choosing already-mated males experience lower reproductive success than those simultaneously choosing unmated males (Alatalo et al. 1981, Stenmark et al. 1988, Johnson et al. 1994).

These "cost-no-compensation" models do not apply to Red-winged Blackbirds because in this species females that choose already-mated males do not have lower reproductive success than those choosing unmated males (Beletsky and Orians 1996, Searcy and Yasukawa 1996). This result argues that polygyny in Red-winged Blackbirds is explained by either a no-cost model or a cost-compensation model. No-cost models are plausible because male Red-winged Blackbirds provide relatively little non-shareable parental care (Beletsky and Orians 1990, Yasukawa et al. 1990), and because females gain some protection from nest predation by nesting near one another (Ritschel 1985, Picman et al. 1988). No-cost models are supported by the results of removal experiments in Pennsylvania that show that females do not prefer to nest on territories with fewer females and do not have increased reproductive success when harem sizes are reduced (Searcy 1988, Searcy and Yasukawa 1995), and by a long-term population study in Washington that found females to have higher reproductive success when settling second or third on a territory than when settling first (Beletsky and Orians 1996). Polygyny in other redwing populations may be more plausibly explained by a cost-compensation model, as for example in Ontario, where removal experiments indicate that females prefer to settle on territories where harem sizes have been lowered (Hurly and Robertson 1985, Pribil and Picman 1996).

The distinction between no-cost and cost-compensation hypotheses, as applied to Red-winged Blackbirds, is not as great as it may seem in that it hinges on whether the cost of polygyny is nonexistent or merely small (Bensch 1997). In either case, the fact that the cost is low or nonexistent is in large part due to the low contribution of male Red-winged Blackbirds to provisioning of offspring. To take the extreme, only 6% of males in Washington feed any of the nestlings on their territories, and only about half of these assist with the first brood to hatch (Beletsky and Orians 1990). A female settling with an already-mated male is thus lowering her chances of receiving help by very little, because those chances are low to begin with. But why is the probability of male help so low? Paternal care may be low because males obtain greater reproductive benefit from advertising for additional mates (Beletsky 1996) or guarding other females on the territory (Whittingham 1994) than from provisioning young. Attracting and guarding additional females would not be options for a male if the species was not polygynous. Thus, low parental care can be thought of as a consequence as well as a cause of polygyny.

What these arguments indicate is that male parental care and the degree of polygyny may coevolve: as the frequency of polygyny rises, the payoff increases for activities such as advertising for additional mates and guarding them once they have settled, and this increased payoff selects for males that put more time into advertisement, courtship, and mate guarding and less into provisioning of young. As males decrease their contribution to parental care, the cost of polygyny decreases, causing the frequency and degree of polygyny to increase, which again increases the payoff for advertisement, courtship, and mate guarding (Searcy and Yasukawa 1989, 1995). If paternal care and polygyny coevolve in this way, a negative association ought to exist between the extent of male parental care and the degree of polygyny. Indeed, this prediction has been confirmed in a cross-species comparison of polygynous passerines (Searcy and Yasukawa 1995).

If the cost of polygyny can coevolve with the degree of polygyny, the polygyny models discussed above are not complete explanations of the evolution of polygyny, because these models assume a given level of cost and do not allow that level to evolve. Accordingly, we propose two new hypotheses to explain the evolution of polygyny in Red-winged Blackbirds in which we assume that the cost of polygyny has evolved due to changes in male behavior.

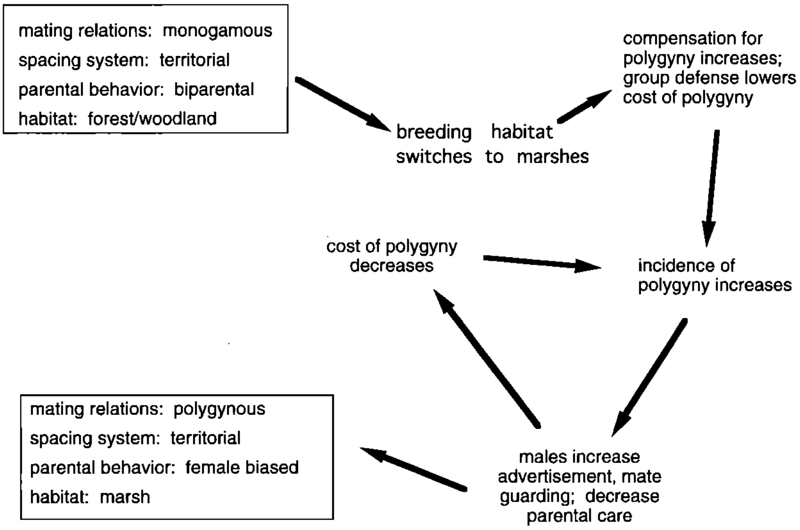

FIG. 1. The first long-term model of the evolution of polygyny in Red-winged Blackbirds. The starting point is an ancestor whose mating system is territorial monogamy, and the ecological change leading to polygyny is a shift in breeding habitat from terrestrial (woodland/forest) to marsh. Modified from Searcy and Yasukawa (1995).

We call these hypotheses "long-term models" because they take a somewhat longer view of polygyny evolution than do the conventional hypotheses.

A key decision in formulating a long-term model concerns the form of the starting point, i.e. the original ancestral mating system. In our first hypothesis, we assume that the starting point is territorial monogamy, the most common mating system in temperate passerines in general. In such a system, the great majority of breeding adults enter into socially monogamous mating relationships, breeding is done on territories defended mainly by the male, and the most important aspect of parental care, provisioning of the young, is shared equally or nearly equally by the male and female. Again following what is probably the norm for temperate passerines, we assume that the breeding habitat is forest or woodland.

Figure 1 offers one scenario for how the mating system of Red-winged Blackbirds might evolve from this particular ancestral system (Searcy and Yasukawa 1995). Change is initiated by a shift in breeding habitat from forest/woodland to marshes. Marsh breeding might increase the incidence of polygyny for a number of reasons. First, in the initial stages of the shift, some males presumably would hold territories in marshes and some in the original habitat, thus creating higher variance in territory quality and a greater likelihood that the polygyny threshold will be exceeded. Second, territories within marshes may vary in quality more than territories in terrestrial habitats (Orians 1969), which again promotes polygyny through polygyny-threshold effects. Third, food may be more plentiful in marshes (Orians 1980), making it easier for females to dispense with male help and thus lowering the cost of polygyny. Finally, group defense against nest predators may be more effective in the smaller territories and more open habitat of marshes (Robinson 1986a), and if so, this would further lower the cost of polygyny. All of these factors might serve to increase the incidence of polygyny only slightly, but a slight increase in polygyny might be enough to put the species into the coevolutionary cycle in which the degree of polygyny increases as the cost of polygyny decreases (Fig. 1). Out of this cycle comes the present Red-winged Blackbird mating system with predominantly polygynous mating relations, parental care skewed toward females, male territoriality, and marsh breeding.

Our second long-term hypothesis assumes an ancestral mating system resembling that of the monogamous congeners of Red-winged Blackbirds (Searcy and Yasukawa 1995). Two species of *Agelaius* have monogamous mating systems. Yellow-winged Blackbirds (*A. thilius*) nest in loose colonies in marshes and ditches, with strictly monogamous pairing relations and no sign of male territoriality (Orians 1980). Yellow-shouldered Blackbirds (*A. xanthomus*) nest in loose colonies (Post 1981). Males are weakly territorial, defending only the area immediately surrounding the nest, but defending these areas before pairing so that they do offer a defended site to prospective mates (Post 1981). The species nests most frequently in mangroves but also in groves of trees in pastures (Post 1981). Provisioning of young is somewhat female-biased in Yellow-winged Blackbirds (Orians 1980) and is equal between the sexes in Yellow-shouldered Blackbirds (Post 1981). We took for our second hypothetical ancestor a mix of features from these two monogamous *Agelaius*, weighted toward features we thought more likely to be primitive. For the spacing system, we assumed no male territoriality, as in the Yellow-winged Blackbird, although the Yellow-shouldered Blackbird is not much different in this regard. For provisioning, we assumed equal sharing, as in the Yellow-shouldered Blackbird. Finally, for breeding habitat, we assumed the ancestor bred in marshes, as in Yellow-winged Blackbirds.

Given this ancestral system, any increase in male territoriality would initiate a change toward polygyny (Fig. 2). Territoriality could increase either because of a demographic change, decreasing intrusion pressure, or because of an ecological change, making resources more defendable. If males increased their defense of space, their territories would begin to take in multiple nesting sites, increasing the chances that more than one female would settle with a given male. Once the frequency of polygyny increases, the species enters the same coevolutionary loop as in the previous hypothesis; out of this loop emerges the redwing mating system.

Additional hypotheses could be formulated by varying either the ancestral mating system or the sequence of events by which the ancestral system is transformed to the present one. Our two hypotheses are therefore just two of the more plausible alternatives out of many. Here, we begin to test between the alternatives using a phylogenetic comparative analysis in which behavioral and ecological traits are mapped onto a phylogeny based on other characters (Brooks and McClennan 1991, Maddison and Maddison 1992). We hope to accomplish three objectives with the analysis: (1) to test between the character sets assumed for the ancestral mating system by the two hypotheses (we call these ancestral systems territorial monogamy and *Agelaius* monogamy, respectively); (2) to

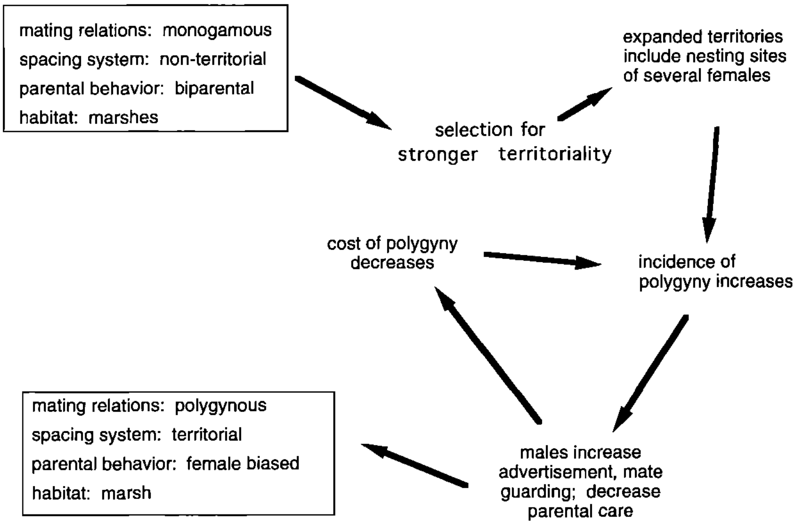

FIG. 2. Second long-term model of the evolution of polygyny in Red-winged Blackbirds. The starting point is a mating system resembling that of monogamous *Agelaius* species (i.e. marsh nesting, non-territorial), and the ecological change leading to polygyny involves selection for stronger territoriality. Modified from Searcy and Yasukawa (1995).

test whether the evolution of polygyny in the ancestors of Red-winged Blackbirds coincides with a shift to marshes, as assumed in our first hypothesis; and (3) to test whether the evolution of unequal parental care coincides with the evolution of polygyny, as assumed in both hypotheses.

METHODS

Our procedure is to map certain behavioral traits of extant species of icterids onto a phylogeny of the family (Lanyon and Omland unpubl. data) and onto a phylogeny of a subset of the family that includes the grackles and allies and to which *Agelaius phoeniceus* belongs (Lanyon and Johnson unpubl. data). These phylogenies have been generated from DNA sequence data and are relatively well resolved with high levels of bootstrap support for many nodes. The Appendix lists the 57 species in the overall data set.

Behavioral-trait evolution was reconstructed using version 3 of MacClade (Maddison and Maddison 1992), which uses parsimony criteria to reconstruct character states at ancestral nodes given the assumed phylogeny and knowledge of character states at terminal nodes (extant species). For our analysis, we assume that the behavioral characters we examine are unordered, meaning that a change between any two states of a given character is possible in a single step. In some species, different individuals or different populations exhibit multiple states of a given character (e.g. marsh and woodland habitat). In such cases, we assigned a single character state when there was a clear majority or preferred state; otherwise we coded the character as polymorphic. We examined five behavioral characters that are noted below. The character states assigned to each species are listed in the Appendix, together with the sources for the evidence.

Mating relations.—This character concerns the association formed between breeding males and females. The possible character states are monogamous, polygynous, and promiscuous. Monogamy is a long-term mating relationship between one male and one female, and a taxon is considered to be monogamous if more than 95% of mating relationships are of this form (Verner and Willson 1966). Polygyny is a long-term relationship between one male and more than one female, and a taxon is considered to be polygynous if more than 5% of mating relationships involve one male and multiple females. Promiscuity is characterized by short-duration associations between males and females and includes species such as Boat-tailed Grackles (*Quiscalus major;* Post 1994, 1995) and Crested Oropendolas (*Psarocolius decumanus;* Tashian 1957, Drury 1962) in which males compete for dominance in the vicinity of colonies of nesting females and dominant males obtain preferential access to females. These systems have also been termed "female-defense polygyny" (Webster 1994).

Spacing behavior.—This character refers to the spacing behavior of males during the breeding season. The possible character states are territorial or non-territorial. In most cases these states are unambiguous, with males either maintaining highly exclusive areas surrounding their nests through aggressive defense, as in Red-winged Blackbirds (Searcy and Yasukawa 1995), or allowing other males to come close to their nests with no sign of aggression, as in Yellow-winged Blackbirds (Orians 1980). Ambiguous cases are ones in which males defend only very small areas surrounding their nests, in which case we used as the criterion for territoriality whether males defended and advertised the nesting area prior to pairing.

Nesting dispersion.—This character refers to the spatial dispersion of nesting females. The character states are dispersed or colonial. The criterion we use for coloniality is that females are more clumped than required by the spatial distribution of their preferred breeding habitat. By this criterion, we consider Red-winged Blackbirds to be non-colonial, because nesting females are widely distributed throughout their preferred marsh habitat.

Preferred nesting habitat.—The possible character states are marsh, grassland, and woodland. The last category includes forest, forest edge, and a variety of habitats with scattered trees, such as mangroves, riparian woodland, and swamps.

Parental care.—We define parental care with respect to the relative contribution of each sex to the provisioning of offspring. The possible character states are equal, meaning that the sexes contribute fairly equally to provisioning; unequal, meaning that males do contribute to feeding young but females contribute substantially more than males; female only, meaning that males take no part in provisioning; and none, meaning that neither parent provisions (i.e. brood parasites).

RESULTS

Figure 3 illustrates the phylogeny for the entire set of 57 species of blackbirds for which DNA data were obtained. At the base of the phylogeny is a polytomy from which five clades emerge. These five clades consist of: (1) the Yellow-billed Cacique (*Amblycercus holosericeus*) only; (2) orioles, genus *Icterus;* (3) meadowlarks (*Sturnella*) and their allies; (4) oropendolas and caciques (*Psarocolius* and *Cacicus*); and (5) grackles (*Quiscalus*) together with a large number of other genera including cowbirds (*Molothrus*) and the various *Agelaius* spe-

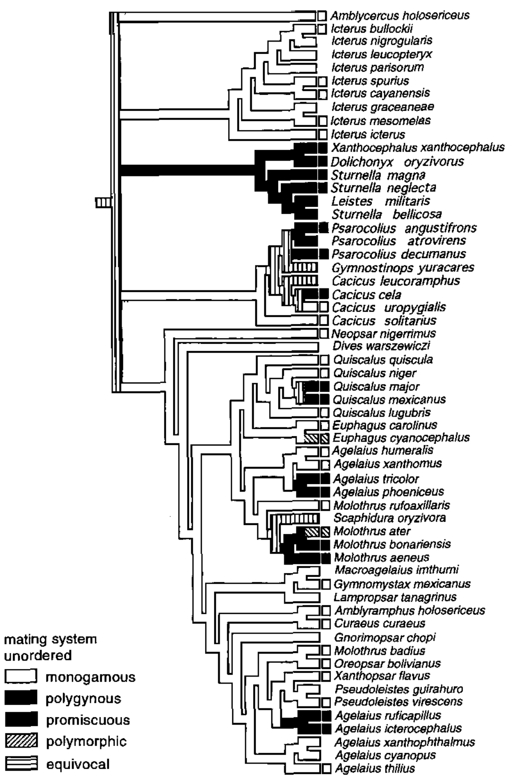

FIG. 3. Mating system character states mapped onto the phylogeny of the entire sample of 57 species of icterids. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

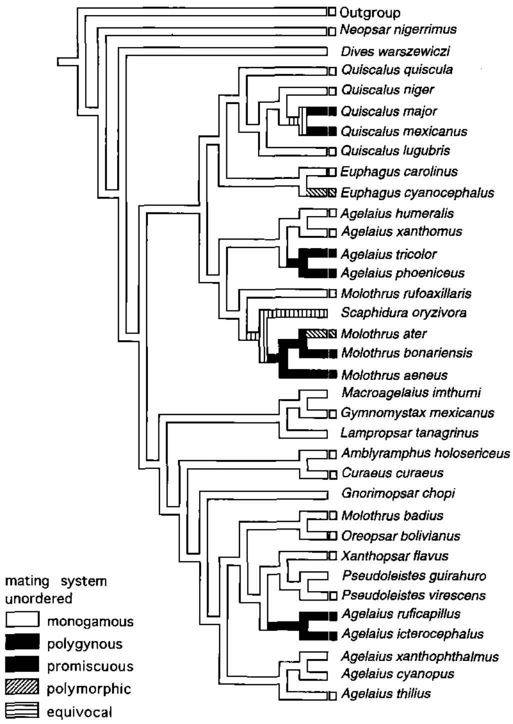

FIG. 4. Mating systems mapped onto the phylogeny of the grackles and allies clade. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

cies. Because the grackle clade contains *Agelaius phoeniceus* and its closest relatives, and because the phylogeny for this clade is so well resolved, we will concentrate on this clade for the remainder of our analysis.

The phylogeny indicates that the genus *Agelaius* is not a monophyletic group (Lanyon 1994). Instead, *Agelaius phoeniceus* appears in a clade together with the second North American *Agelaius* species, *A. tricolor,* and two Caribbean species, *A. humeralis* and *A. xanthomus.* The South American *Agelaius* species appear in a separate clade intermixed with other South American species of the genera *Xanthopsar, Molothrus,* and *Pseudoleistes.*

In mapping the behavioral and ecological traits onto the grackle clade, we assigned to the outgroup those character states that were most common among the four sister clades, i.e. clades 1 to 4 above. The character states assigned to the outgroup are given in the Appendix. The outcome of the analysis of the grackle clade changed very little when this outgroup was omitted.

Mating systems are mapped onto the entire phylogeny in Figure 3 and onto the grackle clade in Figure 4. Mating system is revealed to be a fairly conservative character in the icterids, with polygyny in particular having evolved just four times in the entire family: (1) in the meadowlark clade, (2) in the Great-tailed Grackle (*Quiscalus mexicanus*), (3) in a clade consisting of *Agelaius phoeniceus* and its sister species *A. tricolor,* and (4) in a clade consisting of two South American *Agelaius* species, *A. ruficapillus* and *A. icterocephalus.*

To test between our long-terms models of the evolution of polygyny, we need to reconstruct the characteristics of the closest, non-polygynous ancestor of *A. phoeniceus.* The ancestor at

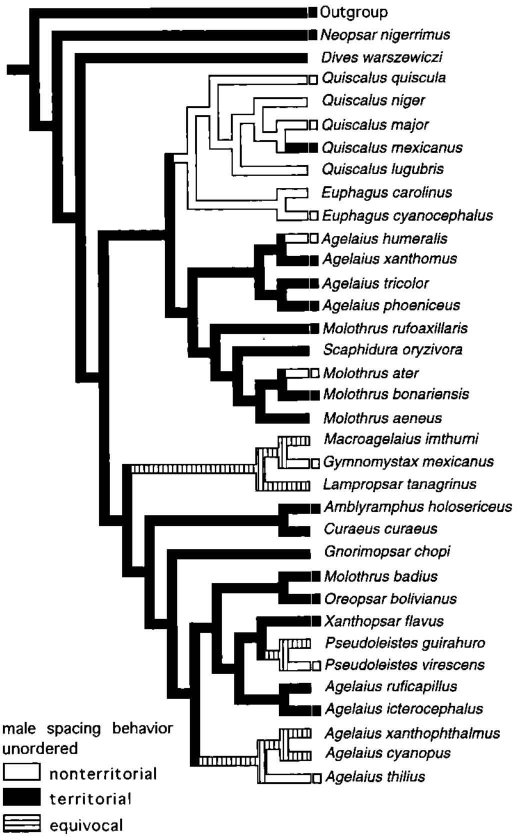

FIG. 5. Male spacing behaviors mapped onto the phylogeny of the grackles and allies clade. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

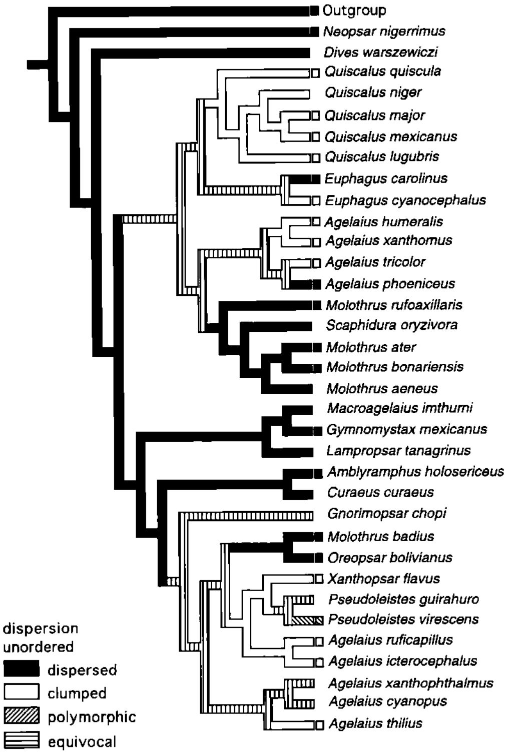

FIG. 6. Female nesting dispersion mapped onto the phylogeny of the grackles and allies clade. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

the node joining redwings with *A. tricolor* is suggested to have been polygynous, but the ancestor at the next node, joining the redwing/tricolor clade with the two Caribbean *Agelaius,* is suggested to have been monogamous (Fig. 4). Thus, polygyny in redwings seems to have evolved from monogamy, as almost all polygyny hypotheses assume. This closest monogamous ancestor of Red-winged Blackbirds is found to have the following characteristics.

Male spacing behavior: territorial (Fig. 5). Territoriality is a primitive trait in the grackle clade, and the monogamous redwing ancestor retains this behavior, as do most of its closest relatives.

Female nesting dispersion: equivocal (Fig. 6). Dispersed nesting is shown to be the primitive state in the grackle clade as a whole, but colonial nesting occurs in many close relatives of *A. phoeniceus,* including the grackles, the two Caribbean *Agelaius* (*A. humeralis* and *A. xanthomus*), and the redwing's sister species, *A. tricolor.*

Preferred nesting habitat: woodland (Fig. 7). A preference for woodlands is primitive in the grackle clade and is retained by most extant species. Marshes have been invaded three times within the grackle clade: once by the *A. phoeniceus/A. tricolor* lineage, once by *Amblyramphus holosericeus,* and once (perhaps twice) by the South American *Agelaius/Pseudoleistes* lineage.

Parental care: equal (Fig. 8). Equal provisioning of nestlings by males and females is found to be the primitive state for this character for the grackle clade as a whole. The monogamous ancestor of *A. phoeniceus* and *A. tricolor* retained

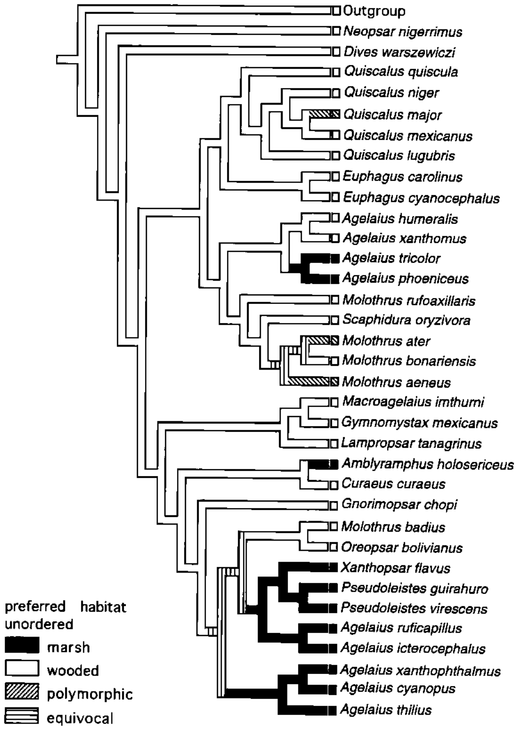

FIG. 7. Preferred nesting habitat mapped onto the phylogeny of the grackles and allies clade. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

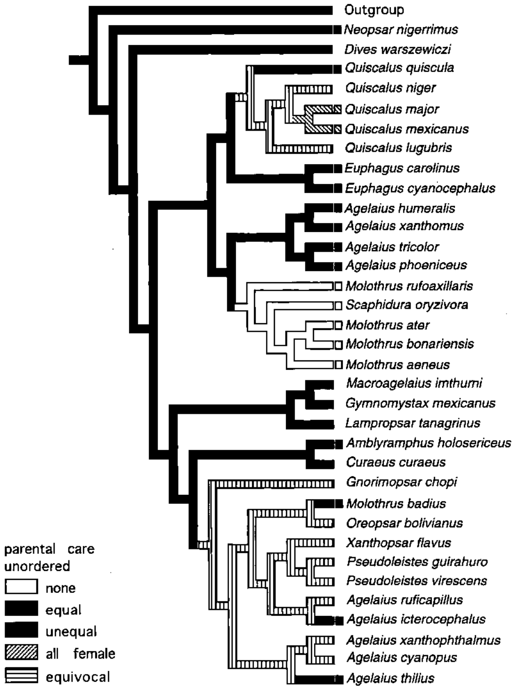

FIG. 8. Patterns of parental care mapped onto the phylogeny of the grackles and allies clade. The squares at the top of the phylogeny show our assignment of character states to extant species; patterns in the rest of the phylogeny are assignments made by MacClade (Maddison and Maddison 1992).

this state. Unequal sharing of parental care is indicated to have evolved at the same time that polygyny and preference for marshes evolved in the joint ancestor of *A. phoeniceus* and *A. tricolor.*

DISCUSSION

The phylogenetic analysis suggests that polygyny in Red-winged Blackbirds evolved from monogamy, and that the most recent monogamous ancestor of redwings was territorial, shared parental care equally between the sexes, and bred primarily in a terrestrial woodland habitat. The analysis cannot discriminate whether breeding females in this monogamous ancestor nested colonially (as in *A. tricolor*) or non-colonially (as in *A. phoeniceus*).

These results are sufficient to disprove our second long-term model for the evolution of polygyny in Red-winged Blackbirds. That model assumes that the present redwing mating system evolved from a monogamous system with non-territorial spacing behavior among males, equal sharing of parental care, and a preference for marsh nesting (Fig. 2). The phylogenetic analysis confirms monogamy and equal parental care as characteristics of the immediate non-polygynous ancestor of redwings but denies the nonterritorial spacing system and the preference for marsh nesting. The rejection of the latter two character states causes us to reject this model.

The results are much more consistent with our first long-term model. This hypothesis assumes that the present mating system evolved from a monogamous system with territorial spacing behavior among males, equal sharing of parental care, and a preference for terrestrial habitats such as forest or woodland (Fig. 1). All of these assumptions are in accord with our reconstruction of the characteristics of the closest non-polygynous ancestor of Red-winged Blackbirds. Moreover, the model suggests that the evolution of the polygynous mating relations and female-biased parental care coincided with the shift from terrestrial to marsh breeding, and this temporal association of character changes is also supported by our results. That is, the phylogenetic analysis suggests that the mating system changed from monogamy to polygyny, parental care changed from equal in the sexes to female-biased, and habitat preference changed from woodlands to marshes, all on the branch that leads up to the immediate ancestor of *A. phoeniceus* and *A. tricolor.*

Orians (1972, 1980) and Robinson (1986a) have suggested that polygyny is correlated with marsh nesting among the icterids, echoing similar suggestions for African ploceids by Crook (1964) and for North American passerines in general by Verner and Willson (1966). According to our results, polygyny originated in marsh-nesting lineages in two of the three instances in which polygyny evolved in the grackle clade. Only a minority of lineages in the clade is or has been polygynous (Fig. 4), so the evolution of polygyny appears to be concentrated in marsh-nesting lineages; however, a concentrated-changes test (Maddison and Maddison 1992) shows that the concentration is not statistically significant ($P = 0.19$). The test cannot be run on the results for the family as a whole because of the occurrence of polytomies in the larger phylogeny (Fig. 3).

Unequal parental care is suggested to have evolved from equal parental care four times in the grackle clade (Fig. 8): (1) Common Grackle (*Quiscalus quiscula*), (2) *A. phoeniceus* / *A. tricolor* clade, (3) Yellow-hooded Blackbird (*A. icterocephalus*) or its ancestors, and (4) Yellow-winged Blackbird or its ancestors. Only in the case of the *A. phoeniceus* / *A. tricolor* clade does the evolution of unequal care clearly coincide with the evolution of polygyny. In the Common Grackle lineage, unequal care definitely evolves in the absence of polygyny because neither the Common Grackle nor its ancestors are or were polygynous. More information is needed on parental care in the relatives of *A. icterocephalus* and *A. thilius* to resolve how unequal care evolved in those lineages. In the larger icterid analysis, unequal care evolves either once or twice in the meadowlark clade (not depicted), but the analysis cannot resolve whether the evolution of polygyny precedes or coincides with the evolution of unequal care. Phylogenetic analysis of additional polygynous groups will be needed to test whether the evolution of unequal care coincides with the evolution of polygyny more often than expected by chance.

In conclusion, the phylogenetic analysis allows us to reconstruct the characteristics of the closest non-polygynous ancestor of Red-winged Blackbirds with some confidence. The results on this ancestor allow us to reject one of our long-term models for the evolution of polygyny in redwings, that assuming a starting point of "*Agelaius* monogamy." The reconstructed character states of this ancestor conform to those assumed in our other hypothesis, the one assuming a starting point of territorial monogamy. Furthermore, the sequence of evolutionary changes found in the reconstruction conforms to the assumptions of the hypothesis, with polygyny evolving on the same branch as marsh nesting and female-biased parental care. What this analysis cannot confirm is the causal part of the hypothesis, i.e. the idea that the change to marsh nesting caused the evolution of polygyny. The causal hypothesis would be better supported if we could show that evolutionary changes to polygyny are concentrated in marsh-nesting lineages, but in our analysis of the grackle clade such a concentration was not statistically significant. Further testing of the causal hypothesis, with a larger sample of evolutionary changes to polygyny, is in order.

Finally, we comment on the relationship between our first long-term model and the standard near-term models of polygyny. Our first model suggests that polygyny initially evolves from territorial monogamy in large part because of cost compensation (or polygyny threshold model) effects; that is, at first females pay a cost of polygyny because of compensation from getting a better territory or male, as envisioned by Verner (1964), Verner and Willson (1966), and Orians (1969). Then, as the cost of polygyny and the degree of polygyny coevolve, the cost of polygyny tends to disappear, so that no-cost models supplant cost-compensation models as the near-term explanation of polygyny (Lightbody and Weatherhead 1988, Searcy and Yasukawa 1989). This idea, that cost-compensation polygyny evolves toward no-cost polygyny, may be applicable to a number of highly polygynous species besides Red-winged Blackbirds, such as Yellow-headed

Blackbirds (*Xanthocephalus xanthocephalus*; Lightbody and Weatherhead 1987, 1988) and Fan-tailed Warblers (*Cisticola juncidis*; Ueda 1984).

ACKNOWLEDGMENTS

We thank those who shared published and unpublished information on the behavior of icterids, including Mike Gochfeld, Bruce Lyon, Viviana Massoni, and especially Gordon Orians.

LITERATURE CITED

ALATALO, R. V., A. CARLSON, A. LUNDBERG, AND S. ULFSTRAND. 1981. The conflict between male polygamy and female monogamy: The case of the Pied Flycatcher *Ficedula hypoleuca*. American Naturalist 117:738–753.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. American Ornithologists' Union, Washington, D.C.

ANKNEY, C. D., AND D. M. SCOTT. 1982. On the mating system of Brown-headed Cowbirds. Wilson Bulletin 94:260–268.

BANCROFT, G. T. 1987. Mating system and nesting phenology of the Boat-tailed Grackle in central Florida. Florida Field Naturalist 15:1–18.

BELETSKY, L. D. 1996. The Red-winged Blackbird: The biology of a strongly polygynous songbird. Academic Press, London.

BELETSKY, L. D., AND G. H. ORIANS. 1990. Male parental care in a population of Red-winged Blackbirds, 1983–1988. Canadian Journal of Zoology 68:606–609.

BELETSKY, L. D., AND G. H. ORIANS. 1996. Red-winged Blackbirds: Decision-making and reproductive success. University of Chicago Press, Chicago.

BELTON, W. 1985. Birds of Rio Grande do Sul, Brazil. Part 2. Formicariidae through Corvidae. Bulletin of the American Museum of Natural History 180:1–242.

BENSCH, S. 1997. The cost of polygyny—Definitions and applications. Journal of Avian Biology 28: 345–352.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and their allies. United States National Museum Bulletin No. 211.

BROOKS, D. R., AND D. A. MCCLENNAN. 1991. Phylogeny, ecology, and behavior: A research program in comparative biology. University of Chicago Press, Chicago.

CARTER, M. D. 1984. The social organization and parasitic behavior of the Bronzed Cowbird in south Texas. Ph.D. dissertation, University of Minnesota, St. Paul.

CLOTFELTER, E. D. 1995. Courtship displaying and intrasexual competition in the Bronzed Cowbird. Condor 97:816–818.

CROOK, J. H. 1964. The evolution of social organization and visual communication in the weaver birds (Ploceidae). Behaviour (Supplement) 10:1–178.

DICKINSON, T. E., J. B. FALLS, AND J. KOPACHENA. 1987. Effects of female pairing status and timing of breeding on nestling productivity in Western Meadowlarks (*Sturnella neglecta*). Canadian Journal of Zoology 65:3093–3101.

DRURY, W. H., JR. 1962. Breeding activities, especially nest building, of the Yellowtail (*Ostinops decumanus*) in Trinidad, West Indies. Zoologica 47: 39–58.

DUFTY, A. M., JR. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99: 316–327.

ELLIOT, P. F. 1980. Evolution of promiscuity in the Brown-headed Cowbird. Condor 82:138–141.

ENSTROM, D. A. 1993. Female choice for age-specific plumage in the Orchard Oriole: Implications for delayed plumage maturation. Animal Behaviour 45:435–442.

FICKEN, R. W. 1963. Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula*. Auk 80:52–72

FLOOD, N. J. 1985. Incidences of polygyny and extra-pair copulation in the Northern Oriole. Auk 102: 410–413.

FRAGA, R. M. 1987. Vocal mimicry in the Epaulet Oriole. Condor 89:133–137.

FRAGA, R. M. 1991. The social system of a communal breeder, the Bay-winged Cowbird *Molothrus badius*. Ethology 89:195–210.

FRIEDMANN, H. 1929. The cowbirds. Thomas Press, Springfield, Illinois.

GIBBS, H. L., P. J. WEATHERHEAD, P. T. BOAG, B. N. WHITE, L. M. TABAK, AND D. J. HOYSAK. 1990. Realized reproductive success of polygynous Red-winged Blackbirds revealed by DNA markers. Science 250:1394–1397.

GOCHFELD, M. 1979. Interspecific territoriality in Red-breasted Meadowlarks and a method for estimating the mutuality of their participation. Behavioral Ecology and Sociobiology 5:159–170.

GRAY, E. M. 1996. Female control of offspring paternity in a western population of Red-winged Blackbirds (*Agelaius phoeniceus*). Behavioral Ecology and Sociobiology 38:267–278.

GROSS, A. O. 1957. Eastern Meadowlark. Pages 53–80 *in* Life histories of North American blackbirds, orioles, tanagers, and allies (A. C. Bent, Ed). United States National Museum Bulletin No. 211.

HOWE, H. F. 1979. Evolutionary aspects of parental care in the Common Grackle, *Quiscalus quiscula* L. Evolution 33:41–51.

HUDSON, W. H. 1920. Birds of La Plata. J. M. Dent and Sons, New York.

HURLY, T. A., AND R. J. ROBERTSON. 1985. Do female Red-winged Blackbirds limit harem size? I. A removal experiment. Auk 102:205–209.

JOHNSON, L. S., L. H. KERMOTT, AND M. R. LEIN. 1994. Territorial polygyny in House Wrens: Are females sufficiently compensated for the cost of polygyny? Behavioral Ecology 5:98–104.

KENNARD, F. H. 1920. Notes on the breeding habits of the Rusty Blackbird in northern New England. Auk 38:412–422.

KNAPTON, R. W. 1988. Nesting success is higher for polygynously mated females than for monogamously mated females in the Eastern Meadowlark. Auk 105:325–329.

KOK, O. B. 1972. Breeding success and territorial behavior of male Boat-tailed Grackles. Auk 89:528–540.

LACK, D. AND J. T. EMLEN, JR. 1939. Observations on breeding behavior in Tricolored Red-wings. Condor 41:225–230.

LANYON, S. M. 1994. Polyphyly of the blackbird genus *Agelaius* and the importance of assumptions of monophyly in comparative studies. Evolution 48:679–693.

LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publications of the Nuttall Ornithological Club No. 1.

LIGHTBODY, J. P., AND P. J. WEATHERHEAD. 1987. Polygyny in the Yellow-headed Blackbird: Female choice versus male competition. Animal Behaviour 35:1670–1684.

LIGHTBODY, J. P., AND P. J. WEATHERHEAD. 1988. Female settling patterns and polygyny: Tests of a neutral-mate-choice hypothesis. American Naturalist 132:20–33.

LYON, B. E. 1997. Spatial patterns of Shiny Cowbird parasitism on Chestnut-capped Blackbirds. Animal Behaviour 54:927–939.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of phylogeny and character evolution. Version 3. Sinauer Associates, Sunderland, Massachusetts.

MARTIN, S. G. 1974. Adaptations for polygyny in the Bobolink, *Dolichonyx oryzivorus*. American Zoologist 14:109–119.

MASON, P. 1987. Pair formation in cowbirds: Evidence found for Screaming but not Shiny cowbirds. Condor 89:349–356.

MILLER, A. H. 1931. Notes on the song and territorial habits of Bullock's Oriole. Wilson Bulletin 43: 102–108.

ORIANS, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecological Monographs 31: 285–312.

ORIANS G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589–603.

ORIANS, G. H. 1972. The adaptive significance of mating systems in the Icteridae. Pages 389–398 *in* Proceedings XV International Ornithological Congress (K. H. Voous, Ed.). The Hague, 1970. E. J. Brill, Leiden, The Netherlands.

ORIANS, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton University Press, Princeton, New Jersey.

ORIANS, G. H. 1983. Notes on the behavior of the Melodious Blackbird (*Dives dives*). Condor 85:453–460.

ORIANS, G. H. 1985. Blackbirds of the Americas. University of Washington Press, Seattle.

ORIANS, G. H., L. ERCKMANN, AND J. C. SCHULTZ. 1977a. Nesting and other habits of the Bolivian Blackbird (*Oreopsar bolivianus*). Condor 79:250–256.

ORIANS, G. H., C. E. ORIANS, AND K. J. ORIANS. 1977b. Helpers at the nest in some Argentine blackbirds. Pages 137–151 *in* Evolutionary ecology (B. Stonehouse and C. Perrins, Eds.). University Park Press, Baltimore, Maryland.

PATTERSON, C. B., W. J. ERCKMANN, AND G. H. ORIANS. 1980. An experimental study of parental investment and polygyny in male blackbirds. American Naturalist 116:757–769.

PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. University of California Publications in Zoology 90:1–115.

PAYNE, R. B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird, in central California. Condor 75:80–99.

PICMAN, J., M. LEONARD, AND A. HORN. 1988. Antipredation role of clumped nesting by marsh-nesting Red-winged Blackbirds. Behavioral Ecology and Sociobiology 22:9–15.

PLEASANTS, B. Y. 1979. Adaptive significance of the variable dispersion pattern of breeding Northern Orioles. Condor 81:28–34.

POST, W. 1981. Biology of the Yellow-shouldered Blackbird—*Agelaius* on a tropical island. Bulletin of the Florida State Museum Biological Sciences 26:125–202.

POST, W. 1994. Are female Boat-tailed Grackle colonies neutral assemblages? Behavioral Ecology and Sociobiology 35:401–407.

POST, W. 1995. Reproduction of female Boat-tailed Grackles: Comparisons between South Carolina and Florida. Journal of Field Ornithology 66: 221–230.

PRIBIL, S., AND J. PICMAN. 1996. Polygyny in the Red-winged Blackbird: Do females prefer monogamy or polygamy? Behavioral Ecology and Sociobiology 38:183–190.

RIDGELY, R. S., AND G. TUDOR. 1989. The birds of South America. University of Texas Press, Austin, Texas.

RITSCHEL, S. E. 1985. Breeding ecology of the Red-winged Blackbird (*Agelaius phoeniceus*): Tests of models of polygyny. Ph.D. dissertation, University of California, Irvine.

ROBINSON, S. K. 1986a. The evolution of social behavior and mating systems in the blackbirds (Icterinae). Pages 175–200 *in* Ecological aspects of social evolution (D. I. Rubenstein and R. W. Wrangham, Eds.). Princeton University Press, Princeton.

ROBINSON, S. K. 1986b. Competitive and mutualistic interactions among females in a Neotropical oriole. Animal Behaviour 34:113–122.

SCHÄFER. E. 1957. Les Conotos: Etude comparative de *Psarocolius angustifrons* et *Psarocolius decumanus*. Bonner Zoologische Beiträge 8:1–151.

SEARCY, W. A. 1988. Do female Red-winged Blackbirds limit their own breeding densities? Ecology 69:85–95.

SEARCY, W. A., AND K. YASUKAWA. 1989. Alternative models of territorial polygyny in birds. American Naturalist 134:323–343.

SEARCY, W. A., AND K. YASUKAWA. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton University Press, Princeton.

SEARCY, W. A., AND K. YASUKAWA. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in Red-winged Blackbirds. Journal of Avian Biology 27:225–230.

SELANDER, R. K. 1965. On mating systems and sexual selection. American Naturalist 99:129–141.

SELANDER, R. K., AND D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed grackles. Condor 63:29–86.

SELANDER, R. K., AND R. J. HAUSER. 1965. Gonadal and behavioral cycles in the Great-tailed Grackle. Condor 67:157–182.

SHORT, L. L. 1975. A zoogeographic analysis of the South American chaco avifauna. Bulletin of the American Museum of Natural History 154:163–352.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna No. 1.

SKUTCH, A. F. 1967. Life history notes on the Oriole-blackbird (*Gymnomystax mexicanus*) in Venezuela. Hornero 10:379–388.

SKUTCH, A. F. 1972. Studies of tropical American birds. Publications of the Nuttall Ornithological Club No. 10.

SKUTCH, A. F. 1996. Orioles, blackbirds, and their kin. University of Arizona Press, Tucson.

STENMARK, G., T. SLAGSVOLD, AND J. T. LIFJELD. 1988. Polygyny in the Pied Flycatcher, *Ficedula hypoleuca*: A test of the deception hypothesis. Animal Behaviour 36:1646–1657.

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

TEATHER, K. L., AND R. J. ROBERTSON. 1986. Pair bonds and factors influencing the diversity of mating systems in Brown-headed Cowbirds. Condor 88:63–69.

UEDA, K. 1984. Successive nest building and polygyny of Fan-tailed Warblers *Cisticola juncidis*. Ibis 126:221–229.

VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Evolution 18:252–261.

VERNER, J., AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143–147.

WEATHERHEAD, P. J., AND P. T. BOAG. 1995. Pair and extra-pair mating success relative to male quality in Red-winged Blackbirds. Behavioral Ecology and Sociobiology 37:81–91.

WEBSTER, M. S. 1994. Female-defence polygyny in a Neotropical bird, the Montezuma Oropendola. Animal Behaviour 48:779–794.

WESTNEAT, D. F. 1993. Polygyny and extra-pair fertilizations in eastern Red-winged Blackbirds (*Agelaius phoeniceus*). Behavioral Ecology 4:49–60.

WHITTINGHAM, L. A. 1994. Additional mating opportunities and male parental care in Red-winged Blackbirds. Animal Behaviour 48:875–883.

WHITTINGHAM, L. A., A. KIRKCONELL, AND L. M. RATCLIFFE. 1996. Breeding behavior, social organization and morphology of Red-shouldered (*Agelaius assimilis*) and Tawny-shouldered (*A. humeralis*) blackbirds. Condor 98:832–836.

WILEY, R. H. 1976. Affiliation between the sexes in Common Grackles. I. Specificity and seasonal progression. Zeitschrift für Tierpsychologie 40: 59–79.

WILEY, R. H., AND A. CRUZ. 1980. The Jamaican Blackbird: A "natural experiment" for hypotheses in socioecology. Evolutionary Biology 13: 261–293.

WILEY, R. H., AND M. S. 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.

WILLIAMS, P. L. 1982. A comparison of colonial and non-colonial nesting by Northern Orioles in central coastal California. M.S. thesis, University of California, Berkeley.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecological Monographs 36: 51–77.

WITTENBERGER, J. F. 1978. The breeding biology of an isolated Bobolink population in Oregon. Condor 80:355–371.

WITTENBERGER, J. F. 1981. Animal social behavior. Duxbury, Boston.

WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84:22–39.

YASUKAWA, K., J. L. MCCLURE, R. A. BOLEY, AND J. ZANOCCO. 1990. Provisioning of nestlings by male and female Red-winged Blackbirds, *Agelaius phoeniceus.* Animal Behaviour 40:153–166.

YOKEL, D. A. 1986. Monogamy and brood parasitism: An unlikely pair. Animal Behaviour. 34:1348–1358.

Associate Editor: J. Ekman

APPENDIX. Species and character states used in the analysis. Dashes indicate character state is unknown.

Species	Mating relations	Spacing behavior	Nesting dispersion	Preferred habitat	Parental care	References[a]
Grackle clade outgroup	Monogamous	Territorial	Dispersed	Wooded	—	
Dolichonyx oryzivorus	Polygamous	Territorial	Dispersed	Grassland	Equal	1, 2, 3
Leistes militaris	—	Territorial	Colonial	Grassland	—	4, 5, 6
Sturnella bellicosa	—	—	—	Grassland	—	6, 7
Sturnella magna	Polygamous	Territorial	Dispersed	Grassland	Unequal	8, 9, 10
Sturnella neglecta	Polygamous	Territorial	Dispersed	Grassland	Unequal	9, 11
Xanthocephalus xanthocephalus	Polygamous	Territorial	Dispersed	Marsh	Unequal	12, 13
Agelaius cyanopus	—	—	—	Marsh	—	5, 6
Agelaius humeralis	Monogamous	Non-territorial	Colonial	Wooded	Equal	6, 14
Agelaius icterocephalus	Polygamous	Territorial	Colonial	Marsh	Unequal	15
Agelaius phoeniceus	Polygamous	Territorial	Dispersed	Marsh	Unequal	16, 17
Agelaius ruficapillus	Polygamous	—	Colonial	Marsh	—	6, 7, 69, 70
Agelaius thilius	Monogamous	Non-territorial	Colonial	Marsh	Unequal	18
Agelaius tricolor	Polygamous	Territorial	Colonial	Marsh	Unequal	19, 20, 21
Agelaius xanthomus	Monogamous	Territorial	Colonial	Wooded	Equal	22
Agelaius xanthophthalmus	—	—	—	Marsh	—	6
Amblyramphus holosericeus	Monogamous	Territorial	Dispersed	Marsh	Equal	6, 18
Amblycercus holosericeus	Monogamous	—	Dispersed	Wooded	—	26
Cacicus cela	Promiscuous	Non-territorial	Colonial	Wooded	Female only	23, 24, 25
Cacicus leucoramphus	—	—	—	Wooded	—	25
Cacicus solitarius	Monogamous	—	—	Wooded	—	6, 25
Cacicus uropygialis	Monogamous	—	Dispersed	Wooded	—	27
Curaeus curaeus	Monogamous	—	—	Wooded	—	6, 25
Dives warszewiczi	—	—	—	Wooded	—	26, 28
Euphagus carolinus	Monogamous	—	Dispersed	Wooded	Equal	29, 30
Euphagus cyanocephalus	Mono/Poly	Non-territorial	Colonial	Wooded	Equal	31, 32
Gnorimopsar chopi	—	—	—	Wooded	—	5, 6
Gymnomystax mexicanus	Monogamous	Non-territorial	Dispersed	Wooded	—	33
Icterus cayanensis	Monogamous	—	—	Wooded	—	34
Icterus cucullatus	—	—	—	Wooded	—	30
Icterus bullockii	Monogamous	Territorial	Dispersed/colonial	Wooded	Equal	35, 36, 37, 38
Icterus graceannae	—	—	—	Wooded	—	25
Icterus icterus	Monogamous	—	—	Wooded	—	5, 7, 25
Icterus leucopteryx	—	—	—	Wooded	—	39
Icterus mesomelas	Monogamous	—	Dispersed	Wooded	—	25, 26
Icterus nigrogularis	—	—	—	Wooded	—	25
Icterus parisorum	—	—	—	Wooded	—	39
Icterus spurius	Monogamous	Territorial	Dispersed/colonial	Wooded	Equal	30, 40
Lampropsar tanagrinus	—	—	—	Wooded	—	25
Macroagelaius imthurni	—	—	—	Wooded	—	6, 26

APPENDIX. Continued.

Species	Mating relations	Spacing behavior	Nesting dispersion	Preferred habitat	Parental care	References[a]
Molothrus aeneus	Promiscuous	—	—	Grass / wooded	None	26, 41, 42
Molothrus ater	Mono / Poly / Prom	Non-territorial	Dispersed	Marsh / grass / wooded	None	43, 44, 45, 46, 47, 48
Molothrus badius	Monogamous	Territorial	Dispersed	Wooded	Equal	49, 50
Molothrus bonariensis	Promiscuous	Territorial	Dispersed	Wooded	None	50, 51
Molothrus rufoaxillaris	Monogamous	Territorial	Dispersed	Wooded	None	7, 51
Nesopsar nigerrimus	Monogamous	Territorial	Dispersed	Wooded	Equal	52
Oreopsar bolivianus	Monogamous	Territorial	Dispersed	Wooded	—	53
Psarocolius angustifrons	Promiscuous	Non-territorial	Colonial	Wooded	Female only	23, 54
Psarocolius atrovirens	—	—	—	Wooded	—	25
Psarocolius decumanus	Promiscuous	Non-territorial	Colonial	Wooded	Female only	55, 56
Pseudoleistes guirahuro	—	—	—	Marsh	—	6, 25
Pseudoleistes virescens	Monogamous	Non-territorial	Dispersed / colonial	Marsh	—	57
Gymnostinops yuracares	—	—	—	Wooded	—	6
Quiscalus lugubris	Monogamous	—	Colonial	Wooded	—	7, 58
Quiscalus major	Promiscuous	Non-territorial	Colonial	Marsh / wooded	Female only	59, 60, 61, 62
Quiscalus mexicanus	Polygamous	Territorial	Colonial	Wooded	Female only	7, 59, 63, 64
Quiscalus niger	Monogamous	—	—	Wooded	—	6, 7
Quiscalus quiscula	Monogamous	Non-territorial	Colonial	Wooded	Unequal	65, 66, 67
Scaphidura oryzivora	—	—	—	Wooded	None	6, 39
Xanthopsar flavus	Monogamous	Territorial	Colonial	Marsh	—	7, 68, 69

[a] (1) Martin 1974; (2) Wittenberger 1978; (3) Wittenberger 1982; (4) Gochfeld 1979; (5) Short 1975; (6) Orians 1985; (7) Skutch 1996; (8) Knapton 1988; (9) Lanyon 1957; (10) Gross 1957; (11) Dickinson et al. 1987; (12) Lightbody and Weatherhead 1987; (13) Willson 1966; (14) Whittingham et al. 1996; (15) Wiley and Wiley 1980; (16) Beletsky 1996; (17) Searcy and Yasukawa 1995; (18) Orians 1980; (19) Orians 1961; (20) Lack and Emlen 1939; (21) Payne 1969; (22) Post 1981; (23) Robinson 1986a; (24) Robinson 1986b; (25) Ridgely and Tudor 1989; (26) Skutch 1954; (27) Skutch 1972; (28) Orians 1983; (29) Kennard 1920; (30) Bent 1958; (31) Williams 1952; (32) Patterson et al. 1980; (33) Skutch 1967; (34) Fraga 1987; (35) Flood 1985; (36) Miller 1931; (37) Pleasants 1979; (38) Williams 1982; (39) AOU 1983; (40) Enstrom 1993; (41) Carter 1984; (42) Clotfelter 1995; (43) Yokel 1986; (44) Teather and Robertson 1986; (45) Elliot 1980; (46) Payne 1973; (47) Ankney and Scott 1982; (48) Dufty 1982; (49) Fraga 1991; (50) Friedmann 1929; (51) Mason 1987; (52) Wiley and Cruz 1980; (53) Orians et al. 1977a; (54) Schäfer 1957; (55) Tashian 1957; (56) Drury 1962; (57) Orians et al. 1977b; (58) Selander 1965; (59) Selander and Giller 1961; (60) Post 1994; (61) Post 1995; (62) Bancroft 1987; (63) Selander and Hauser 1965; (64) Kok 1972; (65) Wiley 1976; (66) Ficken 1963; (67) Howe 1979; (68) Belton 1985; (69) Hudson 1920; (70) Lyon 1997.