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## CONFIDENCE OF PATERNITY AND MALE PARENTAL CARE

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*Abstract.*—We present a theoretical framework in order to understand how the relationship between male parental care and paternity is dependent on the relationship between male parental care and offspring recruitment. When there is an S-shaped relationship between offspring recruitment and the parental care of a single male, we predict a threshold relationship between male parental care and paternity. Tree swallows, monogamous dunnocks, and red-winged blackbirds may follow this pattern. Alternatively, when there is a concave-down relationship between offspring recruitment and male parental care, we predict a continuous (gradual) decline in male parental care in response to decreasing paternity. Studies of noisy miners and polyandrous dunnocks suggest this pattern. Our model illustrates that the relationship between male parental care and paternity is more complex than assumed previously. A predicted adjustment of male parental care in response to paternity must be examined in relation to the effect of male parental care on offspring recruitment and the effect of alternative activities on male fitness.

Male parental care is an energetically costly part of reproduction, and males providing parental care are expected to incur a survival cost (Williams 1966; Ricklefs 1974; Hails and Bryant 1979). Consequently, natural selection should favor males that avoid caring for unrelated offspring (Trivers 1972; Maynard Smith 1977). Multiple paternity within broods has been documented in several species of birds (Gowaty and Karlin 1984; Gavin and Bollinger 1985; Westneat 1987; Brown and Brown 1988; Sherman and Morton 1988; Birkhead et al. 1989; Burke et al. 1989; Gibbs et al. 1990). However, no one has quantitatively described how male parental care within species should change with paternity. Parental investment theory predicts that the level of parental care a male invests in a particular brood should decrease with his paternity in that brood (Trivers 1972). In general, a simple linear relationship has been assumed (Møller 1988). However, a theoretical basis for a linear relationship has not been presented in the literature. We suggest the relationship between male parental care and paternity is more complex, and we present a quantitative theoretical framework to examine the nature of this relationship. In our model, the relationship between male parental care and paternity depends on the fitness benefits of nonparental activities and the relationship between offspring recruitment and male parental care.

We measure parental care as the proportion  $x$  of a male's total time budget that he spends in parental care activities at a particular nest, and we let  $w = w(x)$  be the fitness gained by the male from that nest through offspring recruitment. Three

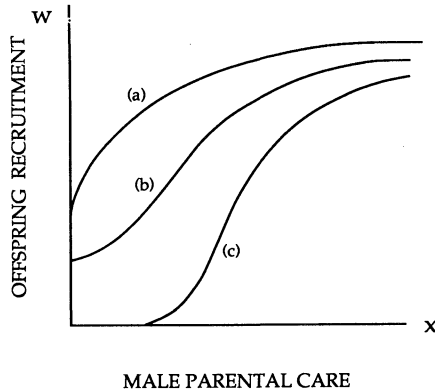


FIG. 1.—Offspring recruitment  $w$  plotted against amount of parental care  $x$  from the male. Three possible forms of this graph are given, a concave-down form ( $a$ ) and two S-shaped forms ( $b$  and  $c$ ). All forms are concave-down for large  $x$ , which reflects the general phenomenon of decreasing marginal returns for large investments. In addition, there are a number of particular hypotheses that might argue for such a form. One of these involves focusing on the cooperative nature of parental care. If at high levels of care, small decreases in care by one parent are more easily compensated for by other parents or helpers than at low levels of care, the slope of the graph should decrease as  $x$  increases, which would cause a concave-down shape. Another model regards offspring recruitment as a simple function of the total parental care (TPC) received from all sources and introduces a fitness deficit  $d$  defined as the amount by which the offspring recruitment falls short of being perfect. Then the hypothesis that each unit of parental care reduces  $d$  by a fixed percentage gives a concave-down  $w$  curve. For altricial species, we expect offspring recruitment as a function of TPC to have the form of  $c$ : it should be zero when TPC is small and will only begin to rise quickly when TPC passes some minimal level for offspring viability. Thus, the positive offspring recruitment shown in  $a$  and  $b$  at  $x = 0$  must reflect the effects of care provided by the female or another male or some helper at the nest. Whether the effect of the male's care on offspring recruitment is initially concave-down ( $a$ ) or concave-up ( $b$ ) depends on the point at which the male's contribution enters the TPC curve.

possible forms for the graph of  $w$  against  $x$  are presented in figure 1: one concave-down form ( $a$ ) and two S-shaped forms ( $b$  and  $c$ ). We let  $p$  be the confidence of the male in his paternity in the brood, and then his total fitness through these offspring will be  $pw(x)$ . Our main result is that the relationship between the optimal level of male parental care  $x$  and his paternity  $p$  is continuous in the concave-down case in figure 1*a* and discontinuous (threshold response) in the S-shaped cases in figure 1*b* and 1*c*.

In our terminology, parental care activities refer to those activities that are directed toward increasing the male's fitness through the offspring of his current brood. Examples include foraging for and feeding the offspring, protecting them from predators, and the parent's engaging in maintenance activities (such as feeding) that will be required in order to perform the parental function. On the other hand, we designate as alternative activities those that are directed toward the production of future broods. Examples include the search for additional mates and extrapair copulations (EPCs) and strategies to increase the survival of the parent over and above the needs of the current brood.

It is important to note that having chosen  $x$ , the male must also decide at what stage in the development of the offspring his time should be invested. We assume that he does this to maximize his overall fitness. There are two factors he may take into account to make this decision: the benefits to the offspring of his parental care and the possible benefits to himself of alternative activities.

There are two cases we consider. In the first case, there is only a single nest, and a male can spend time in parental care activities or in alternative activities. In this case, the male must weigh the possible benefits of the alternate activities in choosing his level of parental care. In the second case, we assume there is more than one nest, and the male's problem is to decide how to divide his parental care among broods with different estimates of paternity.

#### CASE I: A SINGLE NEST

We must specify the rate at which the male will gain fitness through alternative activities. On the whole, the rate of fitness gain through these activities will be different at different times, and if the male could choose these times to coincide with the period of highest fitness gain, then the relationship between fitness gain and time spent in alternative activities would be concave-down. However, any tendency of the male to be more influenced by the needs of the offspring than opportunities elsewhere may reduce the strength of this concavity and make the relationship approximately linear. Our model assumes that the fitness gain through alternative activities is proportional to the amount of time spent in this way. Thus, the total fitness  $W$  of the male is

$$W = pw(x) + b(1 - x),$$

where  $b$  is the rate at which fitness is gained through alternative activities.

To maximize  $W$ , we set  $dW/dx = 0$ , and we get  $w'(x) = b/p$ . Thus, the maximum should occur where the  $w$  graph has slope  $b/p$ . However, this is a local condition that does not distinguish maxima and minima and does not include end-point maxima. An illuminating global argument obtains from working directly with the  $w$  graph. We rewrite  $W$  as

$$W = p \left[ w - \frac{b}{p}x \right] + b,$$

and  $W$  will be a maximum when the expression in the square brackets is a maximum. Geometrically, this is accomplished by choosing  $x$  to maximize the height of the  $w$  graph above any fixed line of slope  $m = b/p$ . The  $x$  at which this occurs is found by drawing the highest possible line with this slope that still has contact with the  $w$  graph, and then the point of contact provides the optimal value of  $x$ , which we write as  $x^*$ .

Figure 2 demonstrates this construction for the cases of a concave-down and an S-shaped graph. There is a qualitative difference between the two cases in the way in which  $x^*$  depends on the ratio  $m = b/p$ . In the concave-down case,  $x^*$  decreases as the ratio  $b/p$  increases, and the possible values of  $x^*$  that can occur

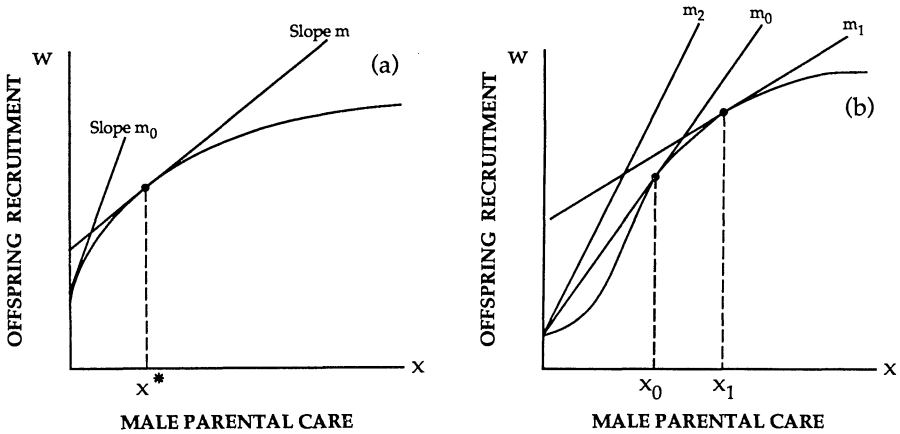


FIG. 2.—The optimal level of parental care  $x^*$  as determined by  $m = b/p$ . Fitness is maximized at the point of contact with the  $w$  graph of a line of slope  $m$  of maximum height that intersects the graph. *a*, Concave-down graph. The optimal point occurs where the slope of the  $w$  graph is equal to the slope of the line. As  $m = b/p$  increases, the line becomes steeper, and  $x^*$  decreases until it becomes and stays zero when  $m = m_0$ , the slope of the  $w$  graph at  $x = 0$ . For  $m > m_0$ ,  $x^* = 0$ . *b*, S-shaped graph. For small values of  $m$  (such as  $m_1$ ) and large values of  $m$  (such as  $m_2$ ), this case behaves like *a*: for  $m = m_1$ ,  $x^* = x_1$ , and for  $m = m_2$ ,  $x^* = 0$ . These two cases are separated by a transitional value  $m_0$ , at which there are two optimal values of  $x$ ,  $x_0$  and 0 (with the same payoff). Values of  $x$  between 0 and  $x_0$  never occur as optima. Thus, at  $m_0$  the optimal  $x$  responds discontinuously to continuous changes in  $m$ . The picture is drawn for the graph of curve *b* in fig. 1, but the configuration is the same for the graph of curve *c* in fig. 1 with the  $m_0$  line drawn from the origin.

form a continuous interval between some maximum value and zero. But in the S-shaped case, although  $x^*$  can take the value of zero and relatively large positive values, it cannot take small positive values. In this case, as the  $b/p$  ratio increases,  $x^*$  decreases continuously, but, at some threshold value of the ratio,  $x^*$  jumps down to zero.

Plots of the optimal value of  $x$  against  $p$  (fig. 3) and  $b$  (fig. 4), with the other parameter held fixed, illustrate the behavior described in figure 2. The optimal level of paternal care generally increases with increasing confidence of paternity and decreases with increasing rate of alternative fitness gain but in a way that is continuous in the concave-down case and discontinuous in the S-shaped case.

CASE 2: MULTIPLE NESTS

We assume the brood fitness functions for each nest are given, as in case 1, by figure 1. Let nest  $i$  have estimate  $p_i$  of paternity, and suppose the male spends time  $x_i$  at this nest where  $\sum x_i = 1$ . The total fitness of the male is now given by the expression

$$\text{Total fitness} = \sum p_i w(x_i).$$

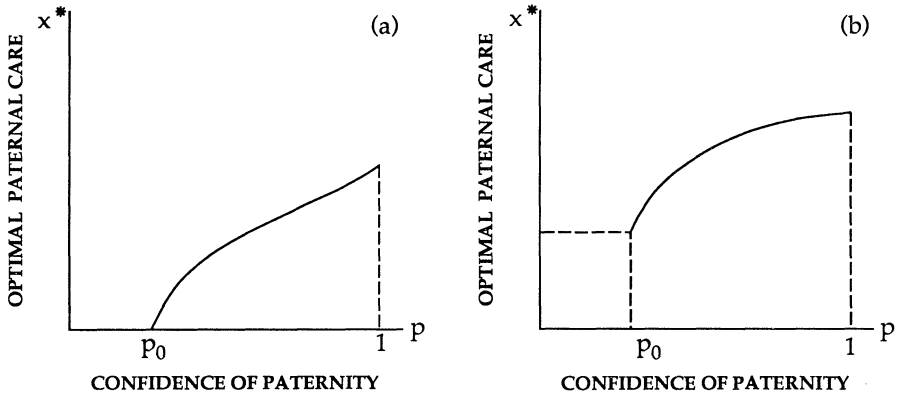


FIG. 3.—The optimal level of male parental care  $x^*$  plotted against the confidence of paternity  $p$ , where we assume that the rate  $b$  of fitness gain from alternative activities stays constant. Figure 3a and b corresponds to the graphs of fig. 2a and b, respectively. In both the concave-down case (a) and the S-shaped case (b),  $x^* = 0$  when  $p < p_0 = b/m_0$  (see fig. 2 for the definition of  $m_0$ ) and is positive and increasing with  $p$  when  $p > p_0$ . In a,  $x^*$  depends continuously on  $p$ , whereas in b,  $x^*$  takes a jump at  $p = p_0$ . The value of  $x$  at this point is the value  $x_0$  defined in fig. 2b.

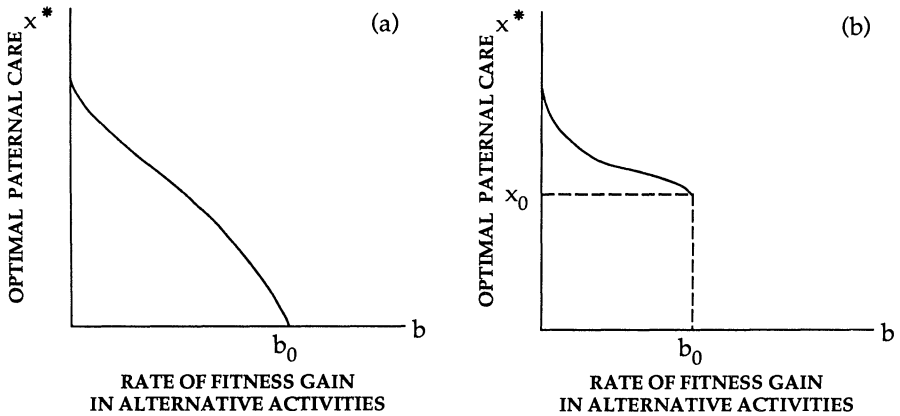


FIG. 4.—The optimal level of male parental care  $x^*$  plotted against the rate  $b$  at which fitness is gained in nonparental activities, where we assume the confidence of paternity  $p$  remains constant. Figure 3a and b corresponds to the graphs of fig. 2a and b, respectively. In both the concave-down case (a) and the S-shaped case (b),  $x^*$  is positive and decreasing with  $b$  when  $b < b_0 = pm_0$  (see fig. 2 for the definition of  $m_0$ ), and  $x^* = 0$  when  $b > b_0$ . In a,  $x^*$  depends continuously on  $b$ , whereas in b,  $x^*$  takes a jump at  $b = b_0$ . The value of  $x$  at this point is the value  $x_0$  defined in fig. 2b.

This can be maximized by the standard method of Lagrange multipliers. The result is that for all nests for which  $0 < x_i < 1$ , we must have

$$w'(x_i) = k/p_i$$

for some constant  $k$ .

We conclude that either the male spends all his time at a single nest (in this case it will be the nest with the highest  $p_i$ ) or he divides his time among more than one nest. In the latter case, the relationship between  $p_i$  and  $x_i$  will be determined by the above equation, and therefore the graph of  $x_i$  against  $p_i$  will have the form of figure 3. That is, the male should spend no time at nests with small  $p_i$ , and for nests with large  $p_i$ , above some threshold value, his time  $x_i$  should increase with  $p_i$ . The form of this increase depends on the form of the fitness function. In the case of a concave-down fitness function,  $x_i$  should increase gradually with  $p_i$ , from zero to some maximum value (fig. 3*a*); in the case of an S-shaped fitness function,  $x_i$  should jump to some nonzero value, then increase gradually with  $p_i$  (fig. 3*b*). In the former case, we might expect to find some nests with quite small values of  $x_i$ , but in the latter case we would not. Rather, we expect to find some nests that are completely ignored and others that receive a substantial amount of paternal care.

#### DISCUSSION

Because male parental care and multiple paternity within a brood are widespread among avian species (Silver et al. 1985; Westneat 1990), it is important to understand how male parental care relates to paternity. We provide a quantitative theoretical framework to examine male parental behavior in relation to paternity and fitness gains from nonparental (alternative) activities. In this model, we illustrate how the optimal level of male parental care invested in a brood in response to decreasing paternity depends on the relationship between offspring recruitment and male parental care. The optimal level of male parental care increases as paternity increases and decreases as the rate of fitness gained from alternative activities increases. This relationship is continuous when the relationship between offspring recruitment and male parental care is concave-down, as in figure 1*a*, and threshold (discontinuous) when the relationship between offspring recruitment and male parental care is S-shaped, as in figure 1*b* and 1*c*. The graphical analysis of these two cases is presented in figures 2, 3, and 4.

We present the concave-down and S-shaped curves as two possible forms for the relationship between offspring recruitment and male parental care. It may be difficult to tell which form applies because in both cases birds may be operating in the concave-down portion of the curve and small changes in paternal care will have similar effects on offspring recruitment. Only with reasonably large reductions in parental care might we be able to distinguish the curves: in the concave-down case, these should result in smaller reductions in recruitment than in the S-shaped case. The form of the relationship between offspring recruitment and male parental care has not been examined in detail for any species (Winkler and Wilkinson 1988), although reductions in male parental care are known to

have greater effects on offspring survival in some species than in others (Wolf et al. 1988; Dunn and Hannon 1989; Hatchwell and Davies 1990).

The S-shaped case appears frequently in the literature (see, e.g., Houston and Davies 1985; Winkler 1987; Winkler and Wilkinson 1988), but the axis on which  $x$  is plotted most often refers to total parental care, and this will include care provided by additional breeders or the female mate. When this relationship is S-shaped, the relationship between recruitment and the care of a single male may still be concave-down if other parental individuals compensate for the reduction in paternal care by any one male. Indeed, the existence of compensating individuals may mean that the male parent being studied only ever operates in the concave-down portion of the curve. However, theoretical and empirical studies suggest that, for a monogamous biparental care system to be stable, any compensation reactions must be incomplete (Houston and Davies 1985). This phenomenon of compensation by other breeders for reduced paternal care may have a major effect on the form of the recruitment curve, and we discuss it more fully.

Rather than look at the reasons for compensatory behavior, we focus on the different possible ways it may affect offspring recruitment. Individuals capable of compensation are additional breeders or the female mate, particularly when breeding conditions are favorable (Hatchwell and Davies 1990; Wright and Cuthill 1990). When male parental care is very low, the slope of the relationship between offspring recruitment and male parental care may depend on the number of individuals compensating for reduced male parental care. For example, one additional breeder or helper may be able to compensate completely until male parental care is reduced by 40%, at which point compensation is no longer complete and total parental care decreases as male parental care decreases, which results in reduced offspring survival. Alternatively, several additional breeders or helpers may be able to compensate completely until male parental care is reduced by 90%. In the latter situation, it would appear that reduced male parental care generally does not affect offspring recruitment. As compensation for reduced male parental care is less and less complete, we expect a relatively greater decline in offspring recruitment when male parental care is very low.

We next discuss the reproductive behavior of several species of birds as examples where male parental care may vary with paternity in the manner described by the theoretical examples above. We emphasize that no data are currently available to provide a rigorous test of this model. However, as examples we have chosen species that are likely to represent each of the two functional relationships between male parental care and paternity when the male has paternity at a single nest or at multiple nests.

### *A Single Nest*

We discuss tree swallows (*Tachycineta bicolor*) as an example where a single male is the resident breeder and care giver at one nest. Studies of male parental behavior in this species suggest that reductions in confidence of paternity have little effect on male parental care until paternity is very low. Resident male tree swallows removed experimentally during egg laying were replaced by other males that could have sired only a small portion of the final brood. These replacement



males fed all nestlings in the brood at a rate similar to that of control males (Robertson 1990). However, when resident males were removed during incubation and replacement males presumably had no paternity in the brood, the replacement males committed infanticide (Robertson 1990). We suggest this switch from full paternal care to infanticide is consistent with the threshold relationship between male parental care and paternity. In this case, we expect the relationship between offspring recruitment and male parental care to be best described by the S-shaped curve. Although offspring survival is highly correlated with male parental care (Leffelaar and Robertson 1986), the shape of the curve is not known.

The dunnock (*Prunella modularis*) provides an example of a breeding system in which there is more than one male breeder and care giver at one nest. In polyandrous breeding trios, two unrelated males share paternity within a brood (Burke et al. 1989). Each male provides parental care in proportion to his paternity, which the male apparently estimates by the amount of time he spends with exclusive access to the female during her fertile period (Burke et al. 1989). Reduced paternity at the nest by one male is paternity gained at the nest by the other male, and a reduction in parental care by one male is compensated for by an increase in parental care provided by the other male (Hatchwell and Davies 1990). Similar compensatory male parental behavior also occurs when one male is removed experimentally (Hatchwell and Davies 1990). The parental behavior of polyandrous male dunnocks is consistent with a continuous relationship between male parental care and paternity. Since reduced parental care by one male is compensated for by an additional breeding male, we expect the relationship between offspring recruitment and male parental care to be described by the concave-down curve.

However, when dunnocks mate monogamously, reductions in paternity (by temporary removal of the male during the female's fertile period) do not influence the level of male parental care (Davies et al., in press). Therefore, the behavior of monogamously mated male dunnocks appears to be consistent with the threshold relationship between male parental care and paternity. When the level of male parental care was reduced experimentally (monogamous males were removed during the nestling period), females increased their provisioning rate, but compensation was incomplete and fledging mass was reduced (Hatchwell and Davies 1990). Therefore, the relationship between offspring recruitment and the parental care of a single male in dunnocks may be S-shaped under monogamy but concave-down under polyandry.

### *Multiple Nests*

In some species of birds, males provide parental care at more than one nest where they have paternity. Red-winged blackbirds (*Agelaius phoeniceus*) and noisy miners (*Manorina melanocephala*) both provide examples where a male breeder provides care at more than one nest. In the former case, he is the only male breeder at these nests, whereas, in the latter case, he shares paternity and parental care with other males.

Male red-winged blackbirds are polygynous (often >2 females/male), and they generally provision nestlings at only one nest at a time in their territories (Yasu-

kawa and Searcy 1982; Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990). Several factors, including brood size (Whittingham 1989), hatching order of nests (Lifjeld and Slagsvold 1990), and paternity, could explain this unequal allocation of male parental care among nests. Paternity is known to vary widely among broods of red-winged blackbirds (Gibbs et al. 1990), but it is not known whether paternity influences the allocation of male parental care. Paternity may be higher in the nest that receives male parental care and lower in the additional nests of a polygynous male where care is not provided. If this is the case, the relationship between male parental care and paternity would be described by the threshold model, and an S-shaped relationship between offspring survival and male parental care would be predicted. Male parental care significantly improves nestling survival because female red-winged blackbirds do not compensate for the absence of male parental care (Muldal et al. 1986; Whittingham 1989; Yasukawa et al. 1990).

In noisy miners, 2–14 males copulate with each female and provision nestlings at each nest (Dow 1977, 1979). Males contribute 50%–93% of all nestling feedings; however, there is a disproportionate amount of paternal care by one male at each nest (Dow 1977). This behavior suggests that the extent of male provisioning is related to the male's genetic investment, specifically, the number of copulations the male had with the female (Dow 1977). This suggests that a continuous relationship between male parental care and paternity is reasonable for noisy miners. Offspring survival is correlated positively with male parental care (Dow and Whitmore 1990). However, shared paternity suggests that additional male breeders may compensate when one male reduces parental care. In this case, we expect the relationship between offspring recruitment and male parental care to be concave-down.

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#### LITERATURE CITED

- Birkhead, T. R., F. M. Hunter, and J. E. Pellatt. 1989. Sperm competition in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour* 38:935–950.
- Brown, C. R., and M. B. Brown. 1988. Genetic evidence of multiple parentage in broods of cliff swallows. *Behavioral Ecology and Sociobiology* 23:379–387.
- Burke, T., N. B. Davies, M. W. Bruford, and B. J. Hatchwell. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* (London) 338:249–251.
- Davies, N. B., B. J. Hatchwell, T. Robson, and T. Burke. In press. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Animal Behaviour*.
- Dow, D. D. 1977. Reproductive behaviour of the noisy miner, a communally breeding honeyeater. *Living Bird* 16:163–185.

- . 1979. The influence of nests on the social behaviour of males in *Manorina melanocephala*, a communally breeding honeyeater. *Emu* 79:71–83.
- Dow, D. D., and M. J. Whitmore. 1990. Noisy miners: variations on the theme of communality. Pages 561–592 in P. B. Stacey and W. D. Koenig, eds. *Cooperative breeding in birds*. Cambridge University Press, Cambridge.
- Dunn, P. O., and S. J. Hannon. 1989. Evidence for obligate male parental care in black-billed magpies. *Auk* 106:635–644.
- Gavin, T. A., and E. K. Bollinger. 1985. Multiple paternity in a territorial passerine: the bobolink. *Auk* 102:550–555.
- 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 hypervariable DNA markers. *Science* (Washington, D.C.) 250:1394–1397.
- Gowaty, P. A., and A. A. Karlin. 1984. Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). *Behavioral Ecology and Sociobiology* 15: 91–95.
- Hails, C. J., and D. M. Bryant. 1979. Reproductive energetics of a free-living bird. *Journal of Animal Ecology* 48:471–482.
- Hatchwell, B. J., and N. B. Davies. 1990. Provisioning of nestlings by dunnocks, *Prunella modularis*, in pairs and trios: compensation reactions by males and females. *Behavioral Ecology and Sociobiology* 27:199–209.
- Houston, A. I., and N. B. Davies. 1985. The evolution of cooperation and life history in the dunnock, *Prunella modularis*. Pages 471–487 in R. Sibly and R. Smith, eds. *Behavioural ecology: the ecological consequences of adaptive behaviour*. Blackwell Scientific, Oxford.
- Leffelaar, D., and R. J. Robertson. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. *Behavioral Ecology and Sociobiology* 18:199–206.
- Lifjeld, J. T., and T. Slagsvold. 1991. Manipulations of male parental investment in polygynous pied flycatchers, *Ficedula hypoleuca*. *Behavioral Ecology* 1:48–54.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25:1–9.
- Møller, A. P. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. *Animal Behaviour* 36:996–1005.
- Muldal, A. M., J. D. Moffatt, and R. J. Robertson. 1986. Parental care of nestlings by male red-winged blackbirds. *Behavioral Ecology and Sociobiology* 19:105–114.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 in R. A. Paynter, ed. *Avian energetics*. Nuttall Ornithological Club, no. 15. Cambridge, Mass.
- Robertson, R. J. 1990. Tactics and counter-tactics of sexually selected infanticide in tree swallows. Pages 381–390 in J. Blondel, A. Gosler, J. D. Lebreton, and R. McCleery, eds. *Population biology of passerine birds: an integrated approach*. Proceedings of the NATO Advanced Workshop, Corsica, 1989. Springer, Berlin.
- Sherman, P. W., and M. L. Morton. 1988. Extra-pair fertilizations in mountain white-crowned sparrows. *Behavioral Ecology and Sociobiology* 22:413–420.
- Silver, R., H. Andrews, and G. F. Ball. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *American Zoologist* 25:823–840.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man 1871–1971*. Aldine, Chicago.
- Westneat, D. F. 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Animal Behaviour* 35:877–886.
- . 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. *Behavioral Ecology and Sociobiology* 27:67–76.
- Whittingham, L. A. 1989. An experimental study of paternal care in red-winged blackbirds. *Behavioral Ecology and Sociobiology* 25:73–80.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687–690.
- Winkler, D. W. 1987. A general model for parental care. *American Naturalist* 130:526–543.
- Winkler, D. W., and G. S. Wilkinson. 1988. Parental effort in birds and mammals: theory and measure-

- ment. Pages 185–214 in P. H. Harvey and L. Partridge, eds. Oxford surveys in evolutionary biology. Vol. 5. Oxford University Press, Oxford.
- Wolf, L., E. D. Ketterson, and V. Nolan, Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Animal Behaviour* 36:1601–1618.
- Wright, J., and I. Cuthill. 1990. Manipulation of sex differences in parental care: the effect of brood size. *Animal Behaviour* 40:462–471.
- Yasukawa, K., and W. A. Searcy. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behavioral Ecology and Sociobiology* 11:13–17.
- Yasukawa, K., J. L. McClure, R. A. Boley, and J. Zanolco. 1990. Provisioning of nestlings by male and female red-winged blackbirds, *Agelaius phoeniceus*. *Animal Behaviour* 40:153–166.

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