The Auk 116(4):1107–1117, 1999

PHYLOGENETIC PATTERNS OF PARENTAL CARE IN CALIDRIDINE SANDPIPERS

OKSANA A. BOROWIK[1] AND DEBORAH A. MCLENNAN[2,3]
[1]*Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada; and*
[2]*Department of Zoology, Centre For Comparative Biology and Biodiversity, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada*

ABSTRACT.—We examined the sequence of parental-care evolution in calidridine sandpipers by mapping parental-care characters onto the two trees produced by a maximum-likelihood and parsimony analysis of molecular data. Our analysis indicated that asymmetric biparental care (male incubates and cares for young, female incubates) is plesiomorphic for the group. This state has been maintained in at least 10 of the 22 species investigated. There have been four changes from the ancestral condition: (1) three to four increases in female care coupled with a complete loss of male care; (2) an increase in female care with the maintenance of male care, producing symmetric biparental care; (3) an increase in female care followed at a later date by three independent losses of male care in *Calidris melanotos, C. fuscicollis,*and *Tryngites subruficollis*; and (4) a decrease in female care in *C. pusilla*. *Received 23 May 1997, accepted 20 April 1999.*

QUESTIONS ABOUT the evolution of avian parental care have fascinated researchers for decades, in part because birds show such a wide range of strategies and because the factors shaping the evolution of these strategies are very complex (Clutton-Brock 1991, Ligon 1993, Ketterson and Nolan 1994, Temrin and Sillén-Tullberg 1994). Given this complexity, one way to disentangle all of the potential factors is to break the system into simple, definable components and model the interactions among them. There are two general scenarios for the sequence of parental-care evolution in Aves. The first (Fig. 1A) proposes that uniparental care always arises from biparental care, with the sex of the single parent being determined by the relative costs and benefits of care versus desertion to each parent (Jenni 1974, Pitelka et al. 1974, Emlen and Oring 1977). Hildén (1975) postulated that the intermediate state between biparental and uniparental care might be a system in which the female rapidly laid two clutches of eggs (double clutching), each clutch being cared for by one parent. Van Rhijn (1985, 1990; see also Handford and Mares 1985) proposed a more complicated scenario (Fig. 1B). In its simplest form, this scenario makes three general predictions: (1) male parental care is the precursor to the radiation of parental-care systems in all birds (van Rhijn 1990:160), (2) female-only care is extremely unlikely to evolve into another care pattern, and (3) biparental care is unlikely to evolve into either type of uniparental care if both parents share incubation duties. Both models make very explicit predictions about the sequence of parental-care evolution that can be examined within a comparative framework.

The phylogenetic comparative approach is a powerful way to disentangle character origin from subsequent character modification and to study the sequence of character modification over long periods of time (Ridley 1983, Wanntorp 1983, Brooks 1985, Brooks and McLennan 1991). One of the strengths of this approach is that it allows the collection of data about the types of evolutionary transitions that happened most often, that happened once and were maintained for long periods of time, and that never happened within a given clade. This information may then be used to examine the predictions of evolutionary models and to highlight areas in the models that need to be modified (Brooks and McLennan 1991, 1994; McLennan 1996).

McKitrick (1992) investigated the macroevolutionary patterns of parental-care origin and diversification across major avian lineages. She concluded that the ancestral parental-care system for Aves was either asymmetric or symmetric biparental care (biparental or female in-

---

[3] Address correspondence to this author. E-mail: mclennan@zoo.utoronto.ca

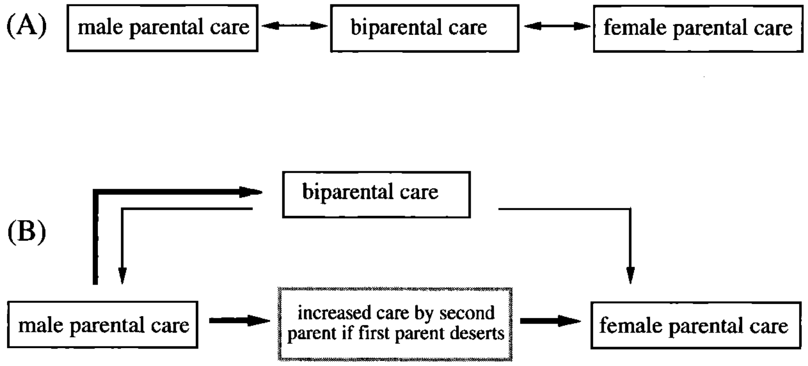

FIG. 1. Pathways of parental-care evolution postulated by (A) Emlen and Oring (1977) and (B) van Rhijn (1990). Bold arrows denote the most probable transitions, and light arrows denote unlikely transitions.

cubation + biparental care of young). In no case did the analysis support the hypothesis that male-only care was the ancestral state for birds. Székely and Reynolds (1995) narrowed the scope of the investigation to one avian lineage, the Charadriides (excluding Labroidea). The macroevolutionary patterns indicated that biparental care (not male-only) was plesiomorphic for this group of shorebirds, reinforcing McKitrick's conclusion that paternal care could not be viewed as the precursor to all other parental-care systems. Within the group, the dominant transitions were male-only to biparental (5 to 11 times), male-only to female-only (6 to 8 times) and biparental to male-only (2 to 6 times). Transitions from biparental to female-only care and vice versa were very rare (0 to 3 times each). The data confirmed previous suggestions of a link between male-only and biparental care and confirmed van Rhijn's (1990) prediction that biparental to female-only care should be rare.

The analysis also highlighted two interesting points for further research. First, there has been a trend toward increasing female care relative to male care in shorebirds. The authors hypothesized that sexual selection favors male desertion because extrapair copulations present the only means open to a male to enhance his reproductive success. Second, the transition "male-only to female-only" care is far more likely to occur than is the sequence "male-only to biparental to female-only" care (see Fig. 1). The only difference between these two transitions is the persistence of the intermediate biparental stage. In the first case, biparental care is transitory from a phylogenetic perspective, although we can infer its presence because male desertion of the clutch presumably could not exist prior to the origin of increased female investment. In the second case, biparental care is detectable on a macroevolutionary scale (still present in extant species). The comparative phylogenetic analysis thus indicated that models of parental-care evolution should incorporate information about the factors influencing the rate of a population's movement through the biparental state into the explanatory framework.

McKitrick (1992) examined patterns of parental care on a large scale, whereas Székely and Reynolds (1995) narrowed their focus to the shorebirds. Continuing in this vein, we investigated the sequence of parental-care evolution within one group of shorebirds, the calidridine sandpipers. We chose this group because relationships within it have been analyzed phylogenetically (Borowik 1996), and because sandpipers display a wide range of parental-care strategies. We were interested mainly in (1) discovering whether the dominant sequences of parental-care evolution within the sandpipers were similar to those detected on a larger phylogenetic scale, and (2) using the power of the comparative phylogenetic approach to highlight areas for future research.

MATERIALS AND METHODS

Data on parental care were obtained from Pitelka et al. (1974), Johnsgard (1981), Székely and Reynolds (1995), and sources listed in the Appendix. As suggested by Temrin and Sillén-Tullberg (1994), we mapped parental-care behavior separately for the

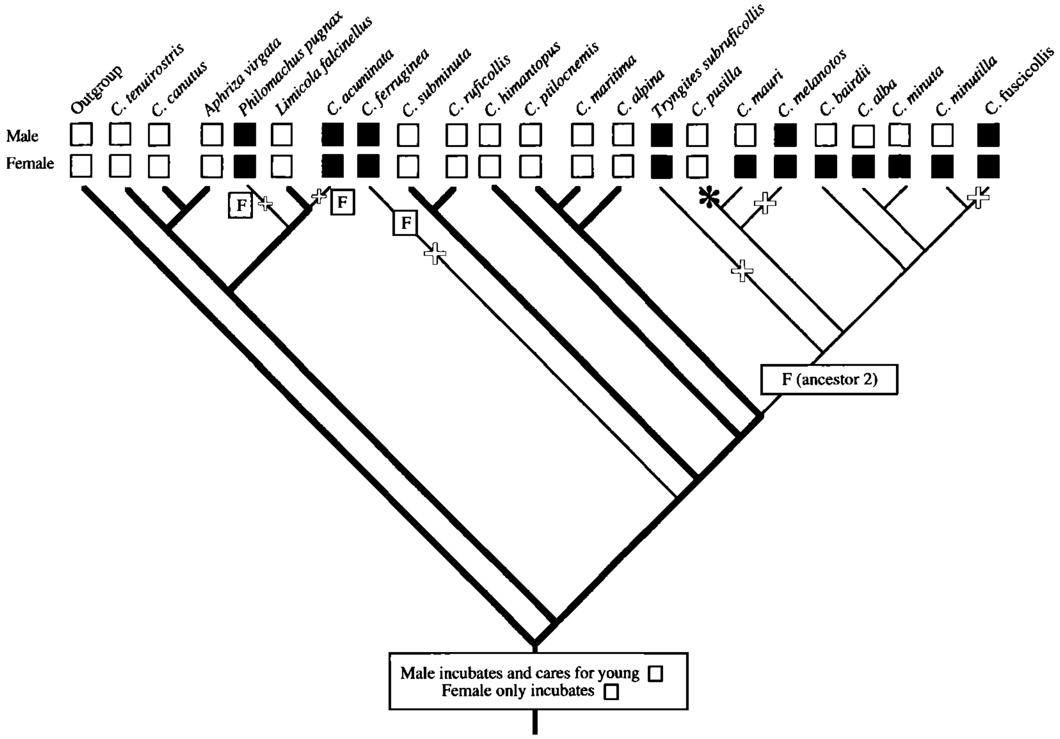

FIG. 2. Parental-care states optimized onto the most-parsimonious tree for calidridine sandpipers based on a maximum-likelihood analysis of 1,645 characters (1,045 base pairs from cytochrome *b*, 600 base pairs from ATPase 6; Borowik 1996). Outgroups = Black Turnstone (*Arenaria melanocephala*) and Ruddy Turnstone (*A. interpres*). Female care: white box = female incubates, black box = female incubates and cares for young; male care: white box = male incubates and cares for young, black box = no male care. Crosses = loss of male parental care, asterisk = reduction in female care, and F = increase in female care. See Figure 5 for the four equally parsimonious optimizations of parental-care evolution in the *Philomachus pugnax* + *Limicola falcinellus* + *C. acuminata* clade.

sexes so that we could study the interaction between different levels of male and female care. Based upon the data collected, we divided parental care into two characters: (1) male care (either male care absent or male incubates and cares for young), and (2) female care (either female incubates or female incubates and cares for young). Parental-care states were coded differently from those listed in Székely and Reynolds (1995) for the following species: (1) female incubation was added to *Calidris alpina, C. canutus, C. maritima, C. pusilla,* and *C. ruficollis;* and female incubation and care for young was added to *C. bairdii, C. mauri,* and *C. minutilla* (see Appendix).

The evolution of parental-care behaviors was examined by optimizing (Farris 1970, Maddison et al. 1984) the behavioral states onto two equally parsimonious molecular-based phylogenetic trees for the calidridine sandpipers (details of tree construction in Borowik 1996). The phylogenetic patterns used in this analysis differ from those used by Székely and Reynolds (1995) in the relationships among members of the genus *Calidris* and also in the addition of *C. minuta, C. ptilocnemis, C. subminuta, C. tenuirostris, Limicola falcinellus, Aphriza virgata,* and *Philomachus pugnax* to the analysis. *Arenaria melanocephala* and *Arenaria interpres* were used as outgroups. Optimizations were checked on McClade 3.01, using the Acctran and Deltran algorithms, but more options were discovered in a hands-on analysis because computer programs did not allow a combination of both Acctran and Deltran optimizations for one character.

RESULTS

Optimizing parental-care states onto both trees indicates that "male incubates and cares for young + female incubates then leaves" is the plesiomorphic condition for parental care in the calidridine sandpipers from which a number of changes in parental care have occurred (Figs. 2 to 4). All optimizations agree

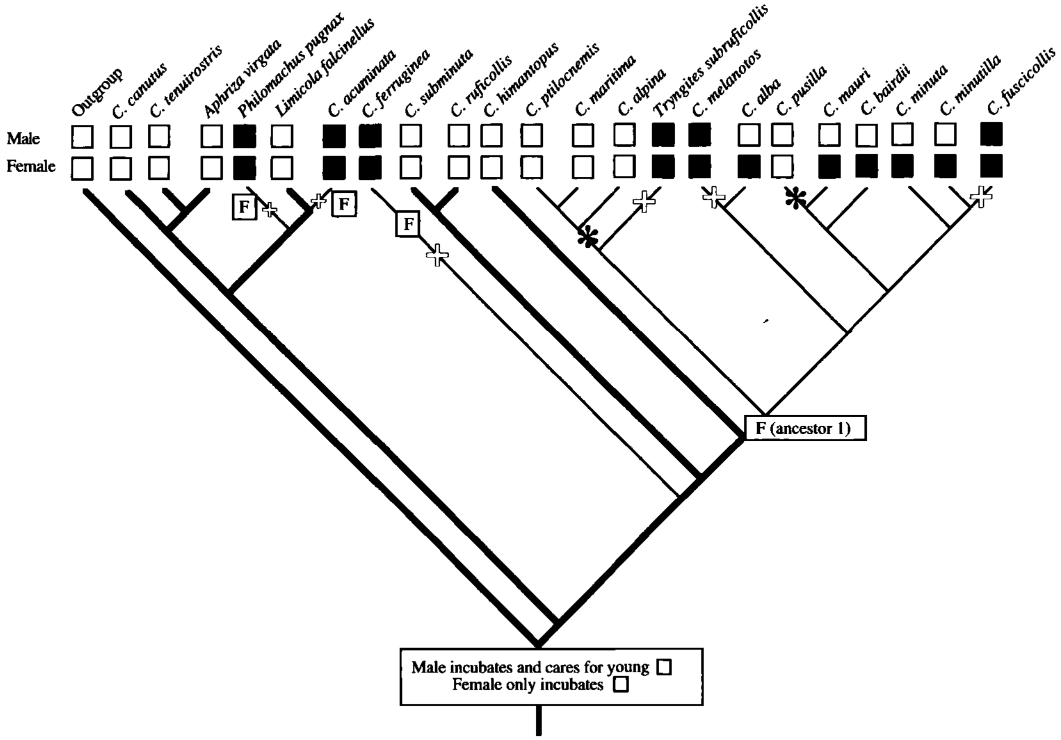

FIG. 3. Parental-care states optimized onto the most-parsimonious tree for calidridine sandpipers based on a parsimony analysis of 1,645 characters (1,045 base pairs from cytochrome *b*, 600 base pairs from ATPase 6; Borowik 1996). See Figure 2 for explanation of symbols.

that (1) an increase in female care is coupled with a loss of male care in *Calidris ferruginea;* (2) loss of male care has occurred independently in *C. melanotos, C. fuscicollis,* and *Tryngites subruficollis;* and (3) loss of male care in *C. melanotos* and *C. fuscicollis* occurred after an increase in female care in a distant ancestor of the two species.

The sequence of events producing the parental system of *T. subruficollis* is ambiguous, as is the position of this species. According to the maximum-likelihood tree (Fig. 2), *T. subruficollis* lost male care following an increase in female care in ancestor 2. One of the optimizations on the maximum-parsimony tree also produces this pattern, although it pushes the origin of an increase in female care back to ancestor 1 (Fig. 3) and, as a consequence, requires that a subsequent decrease in female care occurred in the ancestor of the *C. alpina* + *C. maritima* + *C. ptilocnemis* clade. It is equally parsimonious on the maximum-parsimony tree, however, to suggest that the increase in female care and decrease in male care were coupled in *T. subruficollis* (Fig. 4). Finally, both trees support four equally parsimonious, but complicated, optimizations for the evolution of parental care in the *Philomachus pugnax* + *Limicola falcinellus* + *C. acuminata* clade (Fig. 5).

DISCUSSION

Our results indicate that asymmetric biparental care, with the female incubating and the male both incubating and brooding, is the ancestral condition for calidridine sandpipers. This result mirrors Székely and Reynolds' (1995) conclusions that biparental care is ancestral for the shorebird infraorder Charadriides and does not support van Rhijn's suggestion that male-only care is the precursor to all other forms of parental care in birds (Charadriiformes or otherwise). Our results also indicate that asymmetric biparental care forms a strong ancestral backbone within the clade: 7 to 10 of 22 species retain the symplesiomorphic

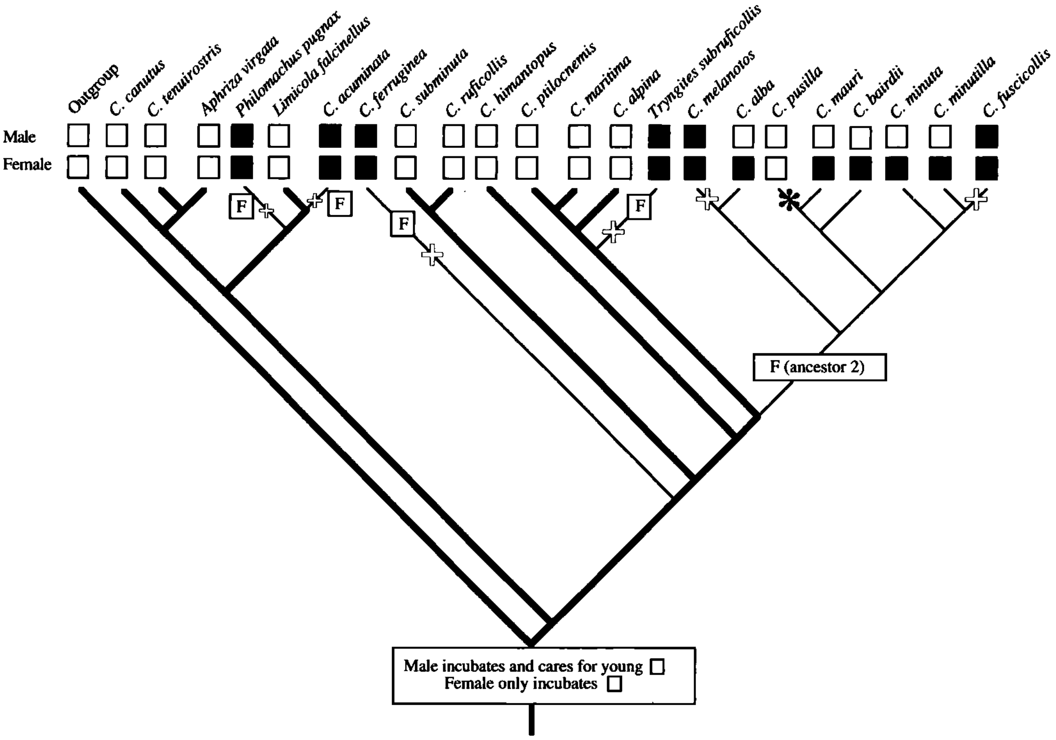

FIG. 4. Deltran optimization of parental-care states on the maximum-parsimony phylogenetic tree for calidridine sandpipers. See Figure 2 for explanation of symbols.

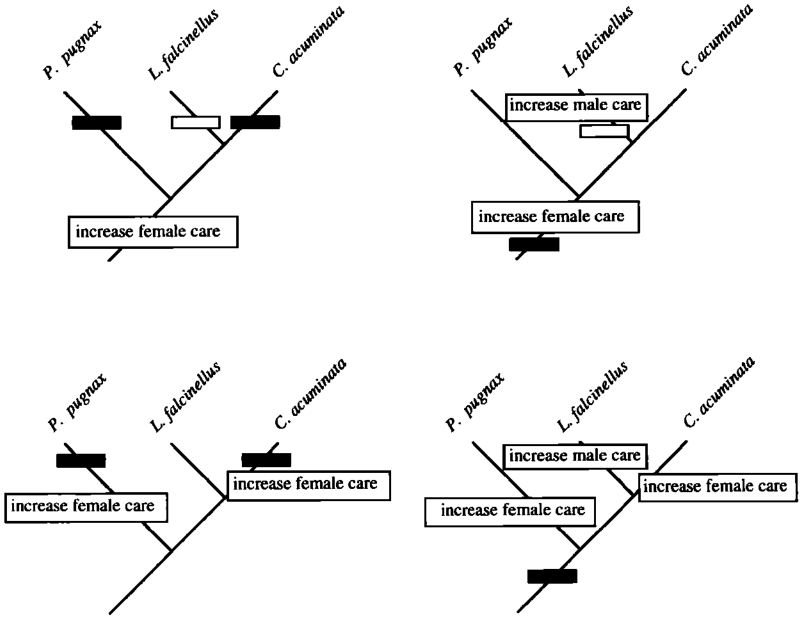

FIG. 5. Four equally parsimonious alternatives for the evolution of parental care in the *Philomachus pugnax* + *Limicola falcinellus* + *C. acuminata* clade. White box = decrease in female care, black box = loss of male care.

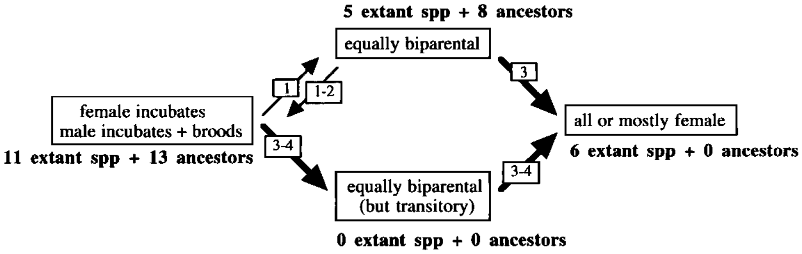

FIG. 6. Evolutionary pathways of parental-care evolution within calidridine sandpipers.

condition (Figs. 2 to 4). Many biologists have tended to focus their attention on differences among species in a group. We believe that it is also important to (1) formulate testable hypotheses about the proportions of a behavioral system that do not change across long periods of time, and (2) document the frequencies of stasis versus divergence in order to determine whether such frequencies are character-specific, clade-specific, or a combination of the two. From the perspective of macroevolutionary patterns, the term "stasis" is used to indicate a lack of change in a particular character across two or more speciation events. The macroevolutionary patterns allow us to recognize a putative case of stasis without implying anything about the underlying mechanisms, which must be sought on genetic, selective, functional, and developmental levels (Carrier 1991, Arnold 1992, McKitrick 1993, Björklund 1996). Recognition of stasis is important, however, because it highlights areas for future research. For example, do similarities occur in ecological conditions, life-history parameters, and/or social structure of the species retaining the symplesiomorphic parental care system that could be operating as stabilizing selection on parental care in these birds? Alternatively, is a portion of the observed stasis an artifact of missing information, or incorrect character coding? Only by collecting these data can we begin to formulate more complete hypotheses of behavioral evolution, hypotheses that can explain both the origin, maintenance (stasis), and divergence of behavioral systems.

Parental care diverges from this ancestral asymmetric biparental backbone in two distinct ways, involving (1) an increase in female parental investment indicated by the origin of female brooding behavior, and (2) a loss of male parental investment. In no case, with the exception of one optimization within the *Philomachus pugnax* + *Limicola falcinellus* + *C. acuminata* clade (Fig. 5, lower right), do the patterns suggest that it is possible to reduce parental care below the amount provided by the symplesiomorphic asymmetric biparental condition. The hypothetical loss of male care in the ancestor of that clade would have produced a population in which only females incubated the eggs and neither parent provided any care for the hatchlings. This ancestor is no longer available for examination, so we can never fully resolve this situation. However, given that none of the other calidridine sandpipers, including the extant members of the *P. pugnax* + *L. falcinellus* + *C. acuminata* clade, displays such a decrease in parental care, the sequence depicted in the lower right of Figure 5 probably represents a situation in which methodological possibility can be discounted on biological grounds.

Although ambiguities exist concerning the exact number of times that female care was increased and male care was lost in calidridines, a consistent pattern emerges within this group of birds. In all cases, the increase in female care to include both incubation of eggs and brooding of young either co-occurred with, or preceded, the loss of male care. These patterns highlight three possible areas for future research. First, all optimizations suggest that one increase in female parental investment is buried deep within the evolutionary history of the calidridine sandpipers; i.e. at least as far back as ancestor 2 (Figs. 2 and 4) and possibly earlier (Fig. 3). This increase in female parental care, to match that already displayed by males, was maintained in the majority of descendants of either ancestor 1 or ancestor 2 (yet more stasis). This suggests that something is different about these descendant species that favored the maintenance of an increase in overall parental investment once it originated. The most obvious places to look for derived changes that might be coupled with this increase in parental care are in the ecology of the parents (e.g. availability of food, length of breeding season, predation pressure) and/or the development of the young (increase in the length of development from the ancestral precocial state; Emlen and Oring 1977, Temrin and Sillén-Tullberg 1995).

Second, all optimizations suggest that the increase in female care was secondarily lost in *Calidris pusilla,* creating a change from symmetric to asymmetric biparental care. Demonstrating that a change in ecology and/or development of the young was correlated with the increase in female care ancestrally, and that the derived ecology and/or development subsequently underwent a reversal correlated with the decrease in female care in *C. pusilla,* would provide strong macroevolutionary evidence for a causal relationship among the variables. Once detected, such macroevolutionary evidence forms the basis for experimental investigations of the hypothesized relationship (McLennan 1996). These patterns also indicate that "asymmetric biparental care" in *C. pusilla* is not homologous with the same state in other calidridine sandpipers. The origin of the asymmetric biparental care system predates the origin of the calidridine sandpipers and thus is buried deep within the phylogenetic history of birds. There are only two ways in which we can reconstruct the forces that shaped the original success of such old systems: (1) examine all of the factors influencing the maintenance of the plesiomorphic trait in extant species, optimize those results onto the tree, and extrapolate backward to the point of origin; or (2) investigate the forces shaping the evolution of the ancestral system if it reappears as a reversal (autapomorphy) in an extant species (Brooks and McLennan 1991, McLennan 1996).

Third, both trees suggest that male parental care has been independently lost in *Tryngites subruficollis, Calidris melanotos* and *C. fuscicollis.* Although studies attempting to document the fitness consequences of removing males from a biparental situation have produced equivocal results, those results tentatively indicate that males may be essential for successful reproduction when they share the incubation duties (Erckmann 1983, Dunn and Hannon 1989, Ketterson and Nolan 1994). In other words, reduction in male care may have a negative effect on male fitness by decreasing the number of viable progeny produced. The fact that paternal investment has been lost in at least three lineages indicates that there must have been a concomitant increase in some other aspect of overall male fitness to balance the negative effect of male desertion on offspring survivorship. For example, freeing males from the bonds of parental care may have been coupled with an increase in the ability of males to pursue alternative reproductive options (Maynard Smith 1977). *Tryngites subruficollis* is a lekking species, *C. fuscicollis* is polygynous, and *C. melanotos* has been described as promiscuous. We are currently investigating the patterns of mating-system evolution in this clade to determine whether the patterns shown by these three species are derived from monogamy. If so, then we will have demonstrated that the ancestral increase in female care created the conditions within which males could be released from parental duties. The creation of such conditions, however, does not explain why males in these particular species were able to exercise that option, nor does it explain why males from many of their close relatives remain bound to their offspring. To disentangle these two issues, we need to collect information about a variety of factors, including the effects of male care on offspring survival, the effect of female-only care on female fecundity, offspring growth patterns, and the availability of fertile females for additional mating attempts by males (Maynard Smith 1977, Ketterson and Nolan 1994).

In summary, the results from our analysis provide strong support for the suggestion that biparental care forms a bridge between predominantly male and predominantly female care. In approximately half of the cases noted, the biparental stage persisted evolutionarily through several speciation events before the transition to female-only care occurred (cf. Fig. 1A). In the other half of the cases, the increase in female care and subsequent loss in male care were coupled phylogenetically, indicating that the transition leading to a dramatic shift in parental care system can occur relatively rapidly (cf. Fig. 1B). These results do not support van Rhijn's (1990) prediction that biparental care is unlikely to evolve into either type of uniparental care if both parents share incubation duties. They do, however, support van Rhijn's (1990) prediction that female-only care is extremely unlikely to evolve into another parental-care pattern. No evidence for the transition "female-only care to male-only care" was uncovered for the shorebirds (Székely and Reynolds 1995, this study), and the transition "female-only care to biparental care" was either absent (this study) or rare (Székely and Reynolds 1995), indicating that male care, once lost, is difficult to evolve again. The overall pattern of symplesiomorphy depicted in Figures 2 to 4 indicates that predominant male care, in the form of asymmetric biparental care, has been very stable throughout the evolutionary history of calidridines. Overall, these patterns are consistent with Maynard Smith's (1977) fundamental insight that forces operating on males and females are evolutionarily interdependent throughout the evolution of parental-care systems and that, within birds, some form of biparental care generally should prevail over mate desertion.

ACKNOWLEDGMENTS

We thank D. R. Brooks, B. Moore, and two anonymous reviewers for their comments on the manuscript. We are particularly grateful to P. Chu for his thoughtful review. This research was funded in part by NSERC operating grants to A. J. Baker and D. A. McLennan.

LITERATURE CITED

ANDREEV, A. V. 1980. A nesting biology study of the Great Knot (*Calidris tenuirostris*) in the River Kolyma basin. Ornitologiya 15:207–208 [in Russian].

ARNOLD, S. J. 1992. Constraints on phenotypic evolution. American Naturalist 140:S85–S107.

ASHKENAZIE, S., AND U. N. SAFRIEL. 1979. Breeding cycle and behavior of the Semipalmated Sandpiper at Barrow, Alaska. Auk 96:56–67.

BENGSTON, S.-A. 1970. Breeding behaviour of the Purple Sandpiper *Calidris maritima* in Western Spitsbergen. Ornis Scandinavica 1:17–25.

BENGSTON, S.-A. 1975. Observations on the breeding biology of the Purple Sandpiper *Calidris maritima*, on Svalbard. Fauna 28:81–86 [in Norwegian].

BJÖRKLUND, M. 1996. The importance of evolutionary constraints in ecological time scales. Evolutionary Ecology 10:423–431.

BOROWIK, O. A. 1996. Molecular systematics and the evolution of mating systems in calidridine sandpipers. Ph.D. thesis, University of Toronto, Toronto, Canada.

BRITTON, D. 1980. Identification of Sharp-tailed Sandpipers. British Birds 73:333–345.

BROOKS, D. R. 1985. Historical ecology: A new approach to studying the evolution of ecological associations. Annals of the Missouri Botanical Garden 72:660–680.

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

BROOKS, D. R., AND D. A. MCLENNAN. 1994. Historical ecology as a research program: Scope, limitations and the future. Pages 1–27 *in* Phylogenetic approaches to ecology (R. I. Vane-Wright and P. Eggleton, Eds.). Academic Press, London.

CARRIER, D. R. 1991. Conflict in the hypaxial musculo-skeletal system: Documenting an evolutionary constraint. American Zoologist 31:644–654.

CARTAR, R. V., AND B. E. LYON. 1988. The mating system of the Buff-breasted Sandpiper: Lekking and resource defence polygyny. Ornis Scandinavica 19:74–76.

CARTAR, R. V., AND R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper: A uniparental incubator in a cold environment. Behaviour 95: 261–290.

CARTAR, R. V., AND R. D. MONTGOMERIE. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. Condor 89:252–260.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.

COOPER, J. M. 1994. Least Sandpiper (*Calidris minutilla*). *In* The birds of North America, no. 115 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

COOPER, J. M., AND E. H. MILLER. 1992. Brood amalgamation and alloparental care in Least Sandpipers, *Calidris minutilla*. Canadian Journal of Zoology 70:403–405.

CRAMP, S., AND K. E. L. SIMMONS (Eds.). 1983. The birds of the western Palearctic. Handbook of the birds of Europe, the Middle East and North Africa. Oxford University Press, Oxford.

DOROGOY, I. V. 1982. Materials on Knot biology on Vrangel Island. Vestnik Zoologii 5:65–69.

DRURY, W. H. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk 78:176–219.

DUNN, P. O., AND S. J. HANNON. 1989. Evidence of obligate male parental care in Black-billed Magpies. Auk 106:635–644.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

ERCKMANN, W. J. 1983. The evolution of polyandry in shorebirds: An evaluation of hypotheses. Pages 113–168 *in* Social behavior of female vertebrates (S. K. Wasser, Ed.). Academic Press, New York.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Systematic Zoology 19:83–92.

FLINT, V. E. 1973. Fauna and ecology of waders. Moscow University Press, Moscow.

FLINT, V. E. 1980. New studies on the biology and distribution of waders. Moscow University Press, Moscow.

GRATTO, C. L., F. COOKE, AND R. I. G. MORRISON. 1983. Nesting success of yearling and older breeders in the Semipalmated Sandpiper *Calidris pusilla*. Canadian Journal of Zoology 61: 1133–1137.

GRATTO, C. L., R. I. G. MORRISON, AND F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102:16–24.

GRATTO-TREVOR, C. L. 1991. Parental care in the Semipalmated Sandpiper, *Calidris pusilla*: Brood desertion by females. Ibis 133:394–399.

GRATTO-TREVOR, C. L. 1992. Semipalmated Sandpiper (*Calidris pusilla*). *In* The birds of North America, no. 6 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

HANDFORD, P., AND M. A. MARES. 1985. The mating systems of ratites and tinamous: An evolutionary perspective. Journal of the Linnean Society of London 25:77–104.

HILDÉN, O. 1975. Breeding system of Temminck's Stint *Calidris temminckii*. Ornis Fennica 52:117–146.

HILDÉN, O. 1978. Occurrence and breeding biology of the Little Stint *Calidris minuta* in Norway [in Swedish]. Anser Supplement 3:96–100.

HOBSON, W. 1972. The breeding biology of the Knot. Proceedings of the Western Foundation of Vertebrate Zoology 2:1–29.

HOGAN-WARBURG, A. J. 1966. Social behaviour of the Ruff, *Philomachus pugnax* (L.). Ardea 54:111–229.

HÖGLUND, J., AND R. V. ALATALO. 1995. Leks. Princeton University Press, Princeton, New Jersey.

HOLMES, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3–46.

HOLMES, R. T. 1971. Density, habitat and mating systems of the Western Sandpiper (*Calidris mauri*). Oecologia 7:191–208.

HOLMES, R. T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87:472–490.

HOLMES, R. T. 1973. Social behaviour of breeding Western Sandpipers (*Calidris mauri*). Ibis 115: 107–123.

HOLMES, R. T., AND F. A. PITELKA. 1962. Behavior and taxonomic position of the White-rumped Sandpiper. Pages 19–20 *in* Proceedings of the 12th Alaskan Science Conference (Science in Alaska, 1961). American Association for the Advancement of Science, College, Alaska.

HOLMES, R. T., AND F. A. PITELKA. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. Auk 81:362–379.

JEHL, J. R., Jr. 1968. The systematic position of the Surfbird *Aphriza virgata*. Condor 70:206–210.

JEHL, J. R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bulletin 85:115–147.

JENNI, D. A. 1974. Evolution of polyandry in birds. American Zoologist 14:129–144.

JOHNSGARD, P. A. 1981. The plovers, sandpipers, and snipes of the world. University of Nebraska Press, Lincoln.

JONSSON, P. A. 1987. Sexual size dimorphism and disassortative mating in the Dunlin *Calidris alpina schinzii* in southern Sweden. Ornis Scandinavica 18:257–264.

KETTERSON, E. D., AND V. NOLAN, Jr. 1994. Male parental behavior in birds. Annual Review of Ecology and Systematics 25:601–628.

LANCTOT, R. B. 1995. A closer look: Buff-breasted Sandpiper. Birding 27:384–390.

LANCTOT, R. B., AND C. D. LAREDO. 1994. Buff-breasted Sandpiper (*Tryngites subruficollis*). *In* The birds of North America, No. 91 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

LIGON, J. D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. Current Ornithology 10: 1–46.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology 33:83–103.

MAYNARD SMITH, J. 1977. Parental investment: A prospective analysis. Animal Behaviour 25:1–9.

MCCAFFERY, B. J. 1983. Breeding flight display in the female White-rumped Sandpiper (*Calidris fuscicollis*). Auk 100:500–501.

MCKITRICK, M. C. 1992. Phylogenetic analysis of avian parental care. Auk 109:828–846.

MCKITRICK, M. C. 1993. Phylogenetic constraint in evolutionary theory: Has it any explanatory power? Annual Review of Ecology and Systematics 24:307–330.

MCLENNAN, D. A. 1996. Integrating phylogenetic and experimental analyses: The evolution of male and female nuptial coloration in the Gasterosteidae. Systematic Biology 45:261–277.

MILLER, E. H. 1979. Functions of display flights by males of the Least Sandpiper (*Calidris minutilla* Vieill.) on Sable Island, Nova Scotia. Canadian Journal of Zoology 57:876–893.

MILLER, E. H. 1983a. Structure of display flights in the Least Sandpiper. Condor 85:220–242.

MILLER, E. H. 1983b. The structure of aerial displays in three species of Calidridinae (Scolopacidae). Auk 100:440–451.

MILLER, E. H. 1985. Parental behaviour in the Least Sandpiper. Canadian Journal of Zoology. 63: 1593–1601.

MILLER, E. H. 1986. Components of variation in nuptial calls of the Least Sandpiper (*Calidris minutilla;* Aves, Scolopacidae). Systematic Zoology 35:400–413.

MILLER, E. H., W. W. H. GUNN, AND S. F. MACLEAN, Jr. 1987. Breeding vocalizations of the Surfbird. Condor 89:406–412.

MYERS, J. P. 1979. Leks, sex, and Buff-breasted Sandpipers. American Birds 33:823–825.

MYERS, J. P. 1980. Territoriality and flocking by Buff-breasted Sandpipers: Variations in non-breeding dispersions. Condor 82:241–250.

MYERS, J. P. 1982. The promiscuous Pectoral Sandpiper. American Birds 36:119–122.

MYERS, J. P., O. HILDÉN, AND P. TOMKOVICH. 1982. Exotic *Calidris* species of the Siberian tundra. Ornis Fennica 59:175–182.

MYERS, J. P., S. L. WILLIAMS, AND F. A. PITELKA. 1980. An experimental analysis of prey availability for Sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Canadian Journal of Zoology 58:1564–1574.

NETTLESHIP, D. N. 1973. Breeding ecology of Turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. Ibis 115:202–217.

NETTLESHIP, D. N. 1974. The breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N.W.T. Polarforschung 44:8–26.

NORTON, D. W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164–176.

PARMELEE, D. F. 1970. Breeding behaviour of the Sanderling in the Canadian High Arctic. Living Bird 9:97–146.

PARMELEE, D. F. 1992. White-rumped Sandpiper (*Calidris fuscicollis*). *In* The birds of North America, no. 29 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

PARMELEE, D. F., W. D. GREINER, AND D. W. GRAUL. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canadian Arctic. Wilson Bulletin 80:5–29.

PARMELEE, D. F., AND R. B. PAYNE. 1973. On multiple broods and the breeding strategy of arctic Sanderlings. Ibis 115:218–226.

PARMELEE, D. F., H. A. STEPHENS, AND R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. National Museum of Canada Bulletin 222:1–229.

PIENKOWSKI, M. W., AND G. H. GREEN. 1976. Breeding biology of Sanderlings in north-east Greenland. British Birds 69:165–177.

PITELKA, F. A. 1959. Numbers, breeding schedules, and territoriality in Pectoral Sandpipers of Northern Alaska. Condor 61:233–264.

PITELKA, F. A., R. T. HOLMES, AND S. F. MACLEAN, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. American Zoologist 14:185–204.

PRATER, A. J. 1972. The ecology of Morecambe Bay III. The food and feeding habits of the Knot (*Calidris canutus* L.) in Morecambe Bay. Journal of Applied Ecology 9:179–194.

PREVETT, J. P., AND J. F. BARR. 1976. Lek behaviour of the Buff-breasted Sandpiper. Wilson Bulletin 88: 500–503.

PRUETT-JONES, S. G. 1988. Lekking versus solitary display: Temporal variations in dispersion of the Buff-breasted Sandpiper. Wilson Bulletin 88: 500–503.

REID, M. L., AND R. D. MONTGOMERIE. 1985. Seasonal patterns of nest defense by Baird's Sandpipers. Canadian Journal of Zoology 63:2207–2211.

RIDLEY, M. 1983. The explanation of organic diversity: The comparative method and adaptations for mating. Clarendon Press, Oxford.

SOIKELLI, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). Annales Zoologici Fennici 4:158–198.

STRAUCH, J. G. 1976. The cladistic relationships of the Charadriiformes. Ph.D. dissertation, University of Michigan, Ann Arbor.

SZÉKELY, T., AND J. D. REYNOLDS. 1995. Evolutionary transitions in parental care in shorebirds. Proceedings of the Royal Society of London Series B 262:57–64.

TEMRIN, H., AND B. SILLÉN-TULLBERG. 1994. The evolution of avian mating systems: A phylogenetic analysis of male and female polygamy and length of pair bond. Biological Journal of the Linnean Society 52:121–149.

TEMRIN, H., AND B. SILLÉN-TULLBERG. 1995. A phylogenetic analysis of the evolution of avian mating systems in relation to altricial and precocial young. Behavioral Ecology 6:296–307.

TOMKOVICH, P. S. 1980. The biology of the Long-toed Stint (*Calidris subminuta*). Ornitologiya 15:104–110 [in Russian].

TOMKOVICH, P. S. 1995. Second report on research on the Great Knot *Calidris tenuirostris* on the breeding grounds. Water Study Group Bulletin 78:50–52.

TOMKOVICH, P. S., AND V. V. MOROZOV. 1980. Breeding biology of the Western Sandpiper (*Calidris mauri*) in Chukotka [in Russian]. Pages 173–175 *in* New studies on the biology and distribution of waders (V. E. Flint, Ed.). University of Moscow, Moscow.

VAN RHIJN, J. G. 1985. A scenario for the evolution of social organization in Ruffs *Philomachus pugnax* and other charadriiform species. Ardea 73:25–37.

VAN RHIJN, J. G. 1990. Unidirectionality in the phylogeny of social organization, with special reference to birds. Behaviour 115:151–173.

WANNTORP, H.-E. 1983. Historical constraints in adaptation theory: Traits and non-traits. Oikos 41: 157–160.

Associate Editor: R. M. Zink

APPENDIX. Sources of information on parental care in calidridine sandpipers. Ruddy Turnstone is the outgroup.

Species	Source
Surfbird (*Aphriza virgata*)	Jehl 1968; Strauch 1976; Miller et al. 1987
Sharp-tailed Sandpiper (*Calidris acuminata*)	Britton 1980
Sanderling (*C. alba*)	Parmelee 1970; Parmelee and Payne 1973; Hildén 1975; Pienkowski and Green 1976; Myers et al. 1980
Dunlin (*C. alpina*)	Holmes 1966; Soikelli 1967; Norton 1972; Jehl 1973; Miller 1983b; Jonsson 1987
Baird's Sandpiper (*C. bairdii*)	Drury 1961; Parmelee et al. 1967; Norton 1972; Myers et al. 1982; Reid and Montgomerie 1985
Red Knot (*C. canutus*)	Hobson 1972; Prater 1972; Nettleship 1974; Dorogoy 1982
Curlew Sandpiper (*C. ferruginea*)	Holmes and Pitelka 1964
White-rumped Sandpiper (*C. fuscicollis*)	Drury 1961; Holmes and Pitelka 1962; Parmelee et al. 1968; McCaffery 1983; Cartar and Montgomeri 1985, 1987; Parmelee 1992
Stilt Sandpiper (*C. himantopus*)	Flint 1973; Jehl 1973; Miller 1983b
Purple Sandpiper (*C. maritima*)	Bengston 1970, 1975
Western Sandpiper (*C. mauri*)	Holmes 1971, 1972, 1973; Tomkovich and Morozov 1980; Myers et al. 1982
Pectoral Sandpiper (*C. melanotos*)	Pitelka 1959; Norton 1972; Myers 1982
Little Stint (*C. minuta*)	Hildén 1978; Cramp and Simmons 1983
Least Sandpiper (*C. minutilla*)	Jehl 1973; Miller 1979, 1983a, b, 1985, 1986; Cooper and Miller 1992; Cooper 1994
Rock Sandpiper (*C. ptilocnemis*)	Myers et al. 1982
Semipalmated Sandpiper (*C. pusilla*)	Norton 1972; Ashkenazie and Safriel 1979; Gratto et al. 1983, 1985; Miller 1983b; Gratto-Trevor 1991, 1992
Red-necked Stint (*C. ruficollis*)	Flint 1980; Myers et al. 1982
Long-toed Stint (*C. subminuta*)	Tomkovich 1980; Myers et al. 1982
Great Knot (*C. tenuirostris*)	Andreev 1980; Flint 1980; Myers et al. 1982; Tomkovich 1995
Broad-billed Sandpiper (*Limicola falcinellus*)	Flint 1973
Ruff (*Philomachus pugnax*)	Hogan-Warburg 1966; Van Rhijn 1985, 1990; Höglund and Alatalo 1995
Buff-breasted Sandpiper (*Tryngites subruficollis*)	Hogan-Warburg 1966; Prevett and Barr 1976; Myers 1979, 1980; Cartar and Lyon 1988; Pruett-Jones 1988; Lanctot and Laredo 1994; Lanctot 1995
Ruddy Turnstone (*Arenaria interpres*)	Parmelee et al. 1967; Nettleship 1973