HYBRIDIZATION AND BREEDING SUCCESS OF COLLARED AND PIED FLYCATCHERS ON THE ISLAND OF GOTLAND

RAUNO V. ALATALO, LARS GUSTAFSSON, AND ARNE LUNDBERG
Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

ABSTRACT.—Two closely related Old World flycatchers, the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*F. albicollis*), are allopatric on most of the European mainland but have overlapping ranges in central and eastern Europe and on the island of Gotland in the Baltic. On Gotland, the Collared Flycatcher is approximately 10 times as abundant as the Pied Flycatcher. The two species hybridize (4% of all matings) at frequencies less than those predicted for random mating (13%). Mixed pairs produce as many offspring as pure Pied Flycatcher pairs and more offspring than Collared Flycatchers. The competence at courtship and/or viability of hybrid offspring, however, is probably reduced, because fewer hybrids breed than would be expected from the proportion of hybrid fledglings.

SPECIES are defined as intrafertile but noninterhybridizing populations, and interspecific hybrids are rarely encountered in most samples of animals under natural conditions. Among birds, interspecific hybrids occur at a frequency of one in about 50,000 (Mayr 1970). We assume that numerous isolating mechanisms owe their existence to selection against interspecific hybridization, which wastes genes. Yet, some bird species pairs remain distinct over much of their common range despite hybridization in certain regions, perhaps especially those regions in which habitats have recently become greatly modified and/or where sympatry is recent (e.g. West 1962, Short 1969, Mayr 1970, Gill 1980). Similarly, largely allopatric species may hybridize in narrow zones of overlap, in which case it is sometimes a matter of taste whether the two are best regarded as species or subspecies. While situations of this kind are commonly described in the literature, quantitative information about the rate of hybridization and the reproductive output of mixed, as opposed to pure, pairs is almost always wanting. Here we report such details for a case of two European allospecies interbreeding in a zone of sympatry.

The species involved are the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*F. albicollis*). These Old World flycatchers occur as allospecies (semispecies), with ranges overlapping in central and eastern Europe and on the Baltic islands of Gotland and Öland (Fig. 1). Sympatric populations hybridize to some extent (Löhrl 1955, Alerstam et al. 1978).

Collared and Pied flycatchers are closely related. Both are highly sex-dimorphic in plumage. Males of the two species are easily distinguished from one another, the male Collared Flycatcher differing from the Pied Flycatcher in having a white collar and rump. On the other hand, females are almost indistinguishable in the field by plumage characters. The songs and alarm calls, however, are highly species-specific.

On the island of Gotland, where this study was performed, the total populations of Collared and Pied flycatchers have recently been estimated at 4,000 and 500 pairs, respectively (Gustafsson and Högström in press). The nearest Collared Flycatcher population is found approximately 600 km southeast of Gotland, while the Pied Flycatcher breeds abundantly on the mainland of northern, central, and eastern Europe (see Fig. 1). Collared Flycatchers thus predominate in this peripheral, isolated area within the range of the more northerly Pied Flycatcher.

In the present paper, we attempt to determine whether or not (1) birds mate assortatively and (2) breeding success of interspecific pairs is reduced, as would be expected for true species.

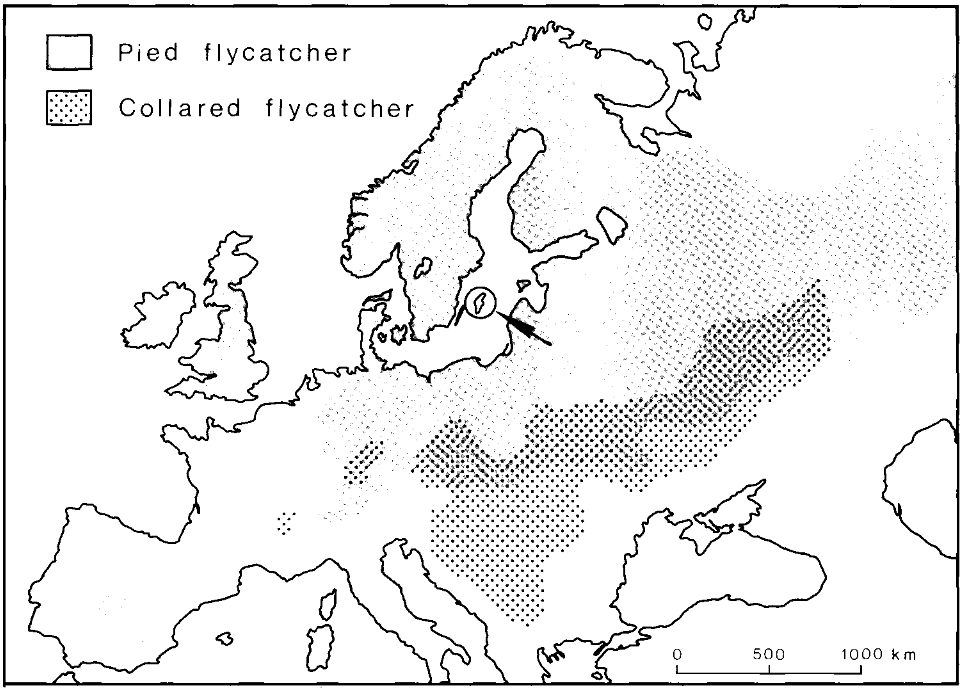

Fig. 1. Breeding ranges of Collared and Pied Flycatchers (based on Alerstam et al. 1978, but modified from Creutz 1970 and Glowacinski 1974). The island of Gotland is encircled.

Study Area and Methods

Collared and Pied flycatchers are especially suitable for study because they use tree holes as nest sites. With nest boxes, one is able to control the whole population, because the birds seldom nest in natural cavities when nest boxes are present. We erected a total of 435 nest boxes in two major forest habitats in southern Gotland (57°10′N, 18°20′E). In deciduous woodlands the nest box density was 6/ha and in coniferous forest, 1.5 nest boxes/ha. The deciduous woodlands are dominated by oak (*Quercus robur*) and ash (*Fraxinus excelsior*), with a dense lower layer of hazel (*Corylus avellana*) and hawthorn (*Crataegus* spp.). The coniferous forest is dominated by pine (*Pinus sylvestris*), but birch (*Betula pubescens*) is also common.

The arrival of the flycatcher males and their occupation of territories were monitored by censuses every second day. For each nest we recorded the onset of laying, clutch size, hatching success, and fledgling numbers. We captured and banded all females and almost all males during the nestling period. In some cases we did not succeed in capturing the male, because polygamous males seldom feed the young of their second nests. The species identity of these males was clear, however, from our census records.

Male hybrids can easily be identified from their vague whitish collars. In the hand, hybrid females can be distinguished by the amount of white on their neck feathers (see Svensson 1975). Collared Flycatcher males were classified as old or yearlings on the basis of the color of all primary coverts (Svensson 1975), while Pied Flycatcher males were aged from the innermost primary covert (Alatalo et al. MS).

Results

Hybridization frequency.—The occupancy of nest boxes and the breeding densities of different pair combinations in the two habitats are given in Table 1. The breeding density of flycatchers was 20 times higher in deciduous than in coniferous forest, and many more nest boxes remained unoccupied in the latter habitat. The Collared Flycatcher was almost 30 times as abundant as the Pied Flycatcher in deciduous forest, while in the coniferous area we found only three times as many Collared Flycatchers. The proportion of mixed pairs was much higher in coniferous forest than in deciduous forest (17% and 2.5%, respectively). In addition, we observed four nests in which

TABLE 1. Breeding densities of Pied (PF) and Collared (CF) flycatchers and of mixed pairs in different habitats on the island of Gotland.

Habitat	Size of study areas (ha)	Number of nest boxes	Percentage occupancy by: Fly-catchers	Percentage occupancy by: All species	Density of flycatcher pairs/ha	Density of breeding pairs/ha: CF × CF	Density of breeding pairs/ha: CF × PF	Density of breeding pairs/ha: PF × PF
Deciduous woodland	37	243	48.6	75.7	3.19	3.00	0.08	0.11
Coniferous woodland	116	192	9.9	24.0	0.16	0.10	0.03	0.03

one parent bird apparently was a hybrid; these pairs are not included in Table 1.

If the individuals of the two species mated randomly, one would expect 13% of the pairs to be mixed (Table 2). The observed proportion of mixed pairs was 4.4%, however, which deviates significantly ($\chi^2 = 7.66$, $P < 0.01$) from random. Thus, there is an overrepresentation of intraspecific matings, interbreeding occurring only in 36% of the number of cases expected if random mating is assumed. We may expect underrepresentation of mixed pairs, simply because the frequencies of occurrence of the two species are not identical in the two habitats. In each habitat, however, the observed number of mixed pairs was 29% (deciduous: $\chi^2 = 5.11$, $P < 0.05$) and 44% (coniferous: $\chi^2 = 2.51$, $P > 0.10$), lower than expected if random mating is assumed. In 5 of the 7 mixed pairs (including 1 pair outside the main study areas), the male was a Collared Flycatcher and the female a Pied Flycatcher. Moreover, of all Pied Flycatchers, 30% were involved in interspecific matings, whereas the corresponding figure for the Collared Flycatcher was only 2%. Of males involved in interspecific mating, 6 out of 7 (86%) were yearlings. For all intraspecific pairs this proportion was lower (55%), but the difference is not significant (Fisher exact, $P = 0.12$).

Breeding success.—Average clutch size and fledgling numbers of intra- and interspecific pairs are given in Table 3. We have combined the data from the two habitats, because we found no differences in breeding success between habitats. Lundberg et al. (1981) found higher breeding success for the Pied Flycatcher in deciduous than in coniferous habitat, but the difference was small. Laying date affects breeding success much more profoundly than habitat, so comparisons must take the time factor into account. Our data are extensive for the Collared Flycatcher, and we therefore use regression equations for clutch size and fledgling numbers versus the laying date of this species as a reference line. The regression equation for clutch size is: $y = -0.078x + 6.77$ (SD $= 0.66$, $n = 123$), where x is laying date (day 1 = 20 May). Pied Flycatchers had, on average, 0.71 (SD $= 0.84$, $n = 7$) more eggs than simultaneously laying Collared Flycatchers (Fig. 2). This difference is significant ($t = 2.70$, $P < 0.01$). The clutch size of mixed pairs was intermediate between that of pure pairs of the two species (0.46 higher than for the Collared Flycatcher, SD $= 0.65$, $n = 7$, $t = 1.81$, $P < 0.10$).

Hatching success of the flycatchers was high, and no difference emerged among the pair combinations (Table 3). The regression line for fledgling numbers of the Collared Flycatcher decreased more rapidly with time than the line for clutch size (Fig. 3; regression equation for number of fledglings: $y = -0.128x + 6.43$, SD $= 1.71$, $n = 123$). Early breeders presumably gained from an outbreak of caterpillars, which levelled off in the second half of June.

TABLE 2. Observed and expected mating combinations of flycatchers.

	Pure Collared Fly-catcher pairs	Pure Pied Fly-catcher pairs	Mixed pairs
Number found	123	7	6
Percentage found	90.4	5.1	4.4
Percentage expected	86.3	1.0	12.7

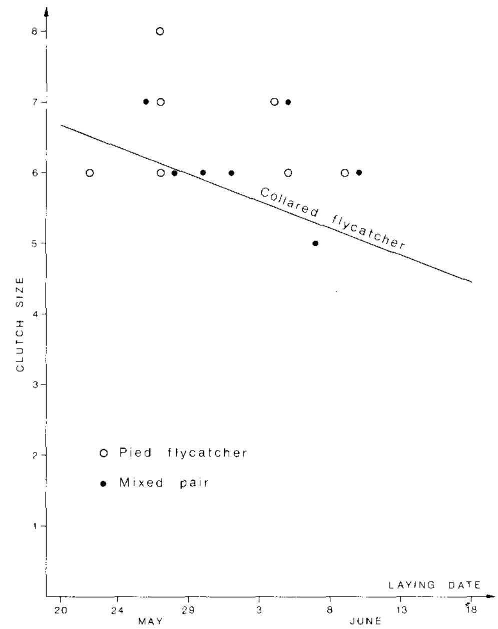

Fig. 2. Clutch size of Pied Flycatchers and of mixed pairs in relation to the regression line for clutch size versus laying date in the Collared Flycatcher.

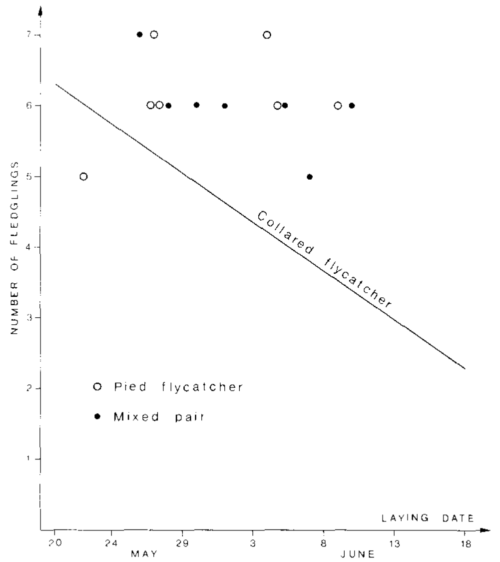

Fig. 3. Number of fledglings of Pied Flycatchers and of mixed pairs in relation to the regression line for fledgling numbers versus laying date in the Collared Flycatcher.

Pied Flycatchers produced, on average, 1.32 (SD = 1.32, $n = 7$) more fledglings than simultaneously breeding Collared Flycatchers (Fig. 3). Unlike clutch-size distributions, the brood-size distributions clearly deviated from normal because of the total failure of some broods. Therefore, t-tests of significance could not be used, and, instead, we calculated for each Collared and Pied flycatcher nest the deviation in fledgling number from that to be expected from the regression line in Fig. 3. In this case, the regression equation is used only to standardize the general decrease in breeding success with season. Between-species differences in terms of such deviations were found to be significant using the Mann-Whitney rank test ($z = 2.17$, $P < 0.05$). Because there is no difference in the mean laying date of the two groups (Table 3), one could compare fledgling numbers discounting the laying date, in which case the difference is still significant (Mann-Whitney; $z = 2.10$, $P < 0.05$). Interspecific pairs were also found to produce significantly more fledglings ($\bar{y} = 1.51$, SD = 0.60, $n = 7$, $z = 2.84$, $P < 0.01$) than simultaneously breeding Collared Flycatchers. No significant difference was found between pure Pied Flycatcher pairs and mixed pairs.

Discussion

In the two flycatcher species, though mixed pairs occur, there is a clear preference for con-

TABLE 3. Breeding data of Pied and Collared flycatchers and of mixed pairs.

Species	n	Mean laying date	Clutch size	SD	Hatched eggs (%)	Fledglings	SD
Collared Flycatcher	123	2 June	5.76	0.81	94.1	4.64	1.90
Pied Flycatcher	7	1 June	6.57	0.79	95.7	6.14	0.69
Mixed pairs	7	3 June	6.14	0.69	100	6.00	0.58

specific mates (Table 2). In two other cases of allospecies hybridization, pairs also mated assortatively [Gill and Murray 1972 (*Vermivora pinus/V. chrysoptera*), Hoffman et al. 1978 (*Larus glaucescens/L. occidentalis*)]. In the latter case, quantitative data were provided. Because only 25% of the *Larus* pairs were pure, the incidence of assortative mating was clearly lower than in this study. In contrast, Ingolfsson (1970) found that *Larus hyperboreus* and *L. argentatus* in Iceland mated randomly.

One would expect marked positive assortative mating if reproductive success of interspecific pairs or of hybrid offspring were low and random mating if hybridization did not reduce reproductive success (Short 1972). Mixed pairs of Collared and Pied flycatchers produced viable offspring. In fact, mixed pairs produced significantly more offspring than Collared Flycatchers (Fig. 2), presumably because the Pied Flycatcher has a larger clutch size than does the Collared Flycatcher (Fig. 2), and most of the mixed pairs involved Pied Flycatcher females.

What happens to the offspring of mixed flycatcher pairs? Hybrids comprised 6.4% of all flycatcher fledglings but only 1.4% of the breeding adults (see also Alerstam et al. 1978). This implies reduced survival or incompetence at courtship. It is not likely that hybrids are less efficient foragers than pure individuals (see Mayr 1970), because the two species are very similar in terms of their foraging habits (Alerstam et al. 1978). On the other hand, the two flycatcher species breeding on Gotland have largely different wintering areas (Moreau 1972), which may cause problems for the hybrids during migration. Hybrid males may be relatively unsuccessful at courtship (Ficken and Ficken 1968, Mayr 1970), because their vocalizations and courtship behavior may differ from the parental species. In fact, the songs of hybrid flycatcher males were clearly different from the songs of the pure species and often included species-specific elements of both the parental species. Also, hybrid female vocalizations differed from those of the parental species.

Offspring from interspecific matings may be fully fertile, may have reduced fertility, or may be sterile (Mayr 1970). For example, captive *Anas platyrhynchos* and *A. acuta* procreated fully fertile hybrids. Hoffman et al. (1978) found high breeding success for hybrids of two *Larus* species under natural conditions. Apparent introgression between several allospecific pairs (for examples, see Anderson 1977) implies that hybrids in many cases are not completely sterile. Brewer (1963; see also Rising 1969) suggested that, in natural populations, hybrids of *Parus atricapillus* and *P. carolinensis* produce less viable offspring. He found a very low fledgling success in six nests in an area of sympatry. Examples of allospecific pairs that produce only F_1 hybrids are given by Anderson (1977). In this study, 2 out of 4 pairs in which hybrids were involved failed to hatch their eggs, while 2 produced young (4 and 6, respectively). In one study plot on the Swedish mainland, (59°50′N, 17°40′E) where the Collared Flycatcher is absent, we found one hybrid male, which was paired with a Pied Flycatcher female. This pair raised four fledglings from six eggs laid. Löhrl (1955) and Vepsäläinen and Järvinen (1977) each found a fertile, breeding, hybrid flycatcher male, but in the latter case the authors mentioned the possibility that the brood could have been adopted by the hybrid male. Thus, in summary, flycatcher hybrids are not fully sterile but apparently do suffer from reduced fertility. Our data are too few to estimate the viability and fertility of hybrids accurately, but, because the two species have retained their specific characters on Gotland so well, introgression can be assumed to be slight.

Alerstam et al. (1978) suggested that hybridization acts as an "agent of competition" between the two flycatcher species on Gotland. Because the Pied Flycatcher is less abundant, a greater proportion of its population will suffer the risk of hybridization (see also Vepsäläinen et al. 1975, Anderson 1977, Vepsäläinen and Järvinen 1977). The considerable rate of hybridization should prevent the Pied Flycatcher from building up its population. The hypothesis is based on the assumption that hybrids are practically sterile. Mixed pairs have high reproductive success, but their hybrid offspring seem to be at a reproductive disadvantage. Our data thus support the hypothesis of Alerstam et al. (1978) in that hybridization may help prevent the Pied Flycatcher from becoming established on Gotland. Conversely, hybridization may limit the ability of the Collared Flycatcher to colonize the north and east European mainland, because the likelihood of hybridization will be very high for a few immigrants (Vepsäläinen et al. 1975). An isolated island like Gotland would be easier to colonize than the mainland, if the Pied Flycatcher were established in Scandinavia before the Collared Flycatcher.

Alerstam et al. (1978) proposed that the small Pied Flycatcher population on Gotland probably is maintained by immigration from the surrounding mainland. We have examined this possibility with the following simple model. We assumed a constant population level of 4,000 Collared Flycatcher pairs and 500 Pied Flycatcher pairs (Gustafsson and Högström in press), a hybridization frequency equivalent to that found in the present study, a 50% adult survival rate to the next year (unpubl. data; see also Anderson 1977), and the same number of offspring per pair of each species surviving to the next breeding season. Then, each year, 73 pairs (=15% of the total population) of Pied Flycatchers have to immigrate to Gotland to compensate for the hybridization losses (if hybridization leads to total reproductive failure). On the other hand, Pied Flycatchers had 32% more fledglings than did the Collared Flycatchers (Table 3). If this difference were maintained until the next breeding, an immigration rate of only 16 Pied Flycatcher pairs per year would be sufficient to retain a stable situation. Because huge numbers of Pied Flycatchers are captured and banded on Gotland during spring migration (Rosvall 1979), an immigration of this modest magnitude may easily be achieved.

The situation is complicated, however, by the fact that the Collared Flycatcher is socially dominant over the Pied Flycatcher (Löhrl 1955). Studies on the Swedish mainland showed that the Pied Flycatcher clearly prefers deciduous forest (Lundberg et al. 1981), but the Collared Flycatcher seems to be able to monopolize the favorable deciduous habitats on Gotland and to relegate the Pied Flycatcher to suboptimal habitats (Table 1). Even if there were no hybridization, we believe that the Collared Flycatcher would survive in its isolated northerly refuge. On the other hand, hybridization may be the prime factor preventing the Collared Flycatcher from establishing a population on the surrounding mainland. One can only speculate about the origin of the present stable distribution of the two species in Scandinavia, but the isolated position of Gotland and the occurrence of hybridization may well be of importance.

ACKNOWLEDGMENTS

We are grateful to T. Alerstam, F. B. Gill, O. Järvinen, S. Ulfstrand, and K. Vepsäläinen for valuable criticism of the manuscript. The work was supported by grants (to S. Ulfstrand) from the Swedish Natural Science Research Council.

LITERATURE CITED

ALERSTAM, T., B. EBENMAN, M. SYLVÉN, S. TAMM, & S. ULFSTRAND. 1978. Hybridization as an agent of competition between two bird allospecies: *Ficedula albicollis* and *F. hypoleuca* on the island of Gotland in the Baltic. Oikos 31: 326–331.

ANDERSON, R. F. V. 1977. Ethological isolation and competition of allospecies in secondary contact. Amer. Natur. 111: 939–949.

BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. Auk 80: 9–47.

CREUTZ, G. 1970. Dringt der Halsbandschnäpper nach Norden vor? Falke 10: 334–339.

FICKEN, M. S., & R. W. FICKEN. 1968. Courtship of Blue-winged Warblers and their hybrids. Wilson Bull. 80: 161–172.

GILL, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97: 1–18.

———, & B. G. MURRAY, JR. 1972. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. Evolution 26: 282–293.

GLOWACINSKI, Z. 1974. Ekspansja mucholowki bialoszyjej, *Ficedula albicollis* (Temm.) w Europie środkowej. Przeglad Zool. 18: 471–484.

GUSTAFSSON, L., & S. HÖGSTRÖM. In press. Hur många fåglar häckar på Gotland? Bläcku.

HOFFMAN, W., J. A. WIENS, & J. M. SCOTT. 1978. Hybridization between gulls (*Larus glaucescens* and *L. occidentalis*) in the Pacific Northwest. Auk 95: 441–458.

INGOLFSSON, A. 1970. Hybridization of Glaucous Gulls *Larus hyperboreus* and Herring Gulls *L. argentatus* in Iceland. Ibis 112: 340–362.

LÖHRL, H. 1955. Beziehungen zwischen Halsband- und Trauerfliegenschnäpper (*Muscicapa albicollis* und *M. hypoleuca*) in demselben Brutgebiet. Acta 11th Congr. Intern. Ornithol. 1954 (Basel): 333–336.

LUNDBERG, A., R. V. ALATALO, A. CARLSON, & S. ULFSTRAND. 1981. Biometry, habitat distribution and breeding success in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 12: 68–79.

MAYR, E. 1970. Animal species and evolution. Cambridge, Massachusetts, Harvard Univ. Press.

MOREAU, R. E. 1972. The Palaearctic-African bird migration systems. London, Academic Press.

Rising, J. D. 1969. A multivariate assessment of interbreeding between the chickadees, *Parus atricapillus* and *P. carolinensis*. Syst. Zool. 17: 160–169.

Rosvall, S. 1979. Halsbandsflugsnapparens *Ficedula albicollis* ankomst till Gotland och Öland våren 1979. Bläcku 5: 73–78.

Short, L. L. 1969. Taxonomic aspects of avian hybridization. Auk 86:84–105.

———. 1972. Hybridization, taxonomy and avian evolution. Ann. Missouri Bot. Garden 59: 447–453.

Svensson, L. 1975. Identification guide to European passerines. Stockholm, Naturhistoriska Riksmuseet.

Vepsäläinen, K., & O. Järvinen. 1977. Ein Bastard-Männchen Halsband-Trauerschnäpper (*Ficedula albicollis* × *F. hypoleuca*) brütet in Finnland. J. Ornithol. 118: 436–437.

———, ———, K. Keynäs, & P. Salminen. 1975. Sepelsiepot *Ficedula albicollis* Hankoniemellä 1971-74. Lintumies (Helsinki) 10: 118–122.

West, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk 79: 339–424.

REVIEWERS FOR THE AUK, 1980–1981

The Auk is fortunate to benefit from the services of many individuals who act as reviewers of manuscripts that are submitted. Their efforts are considerable, and their care and constructiveness continue to impress me as an Editor and as a sometime author. The individuals listed below helped make publication of a journal with high scientific and scholarly standards possible; my thanks to all of them.

Individuals who have contributed reviews of two or more manuscripts are indicated by an asterisk.

Ian Abbott, David G. Ainley, John Alcock*, Thomas Alerstam, Dean Amadon, Daniel W. Anderson, Ted R. Anderson, C. Davison Ankney, Einar Arnason, John C. Avise, Robert O. Bailey, Allan Baker, Myron C. Baker, Robert J. Baker, George S. Bakken, Russell P. Balda, Thomas G. Balgooyen*, David F. Balph, Martha Balph*, Richard C. Banks*, Luis F. Baptista*, George F. Barrowclough*, George A. Bartholomew, Jr., Thomas S. Baskett, Range Bayer*, Jeff Baylis, Michael Beecher*, Colin Beer*, Marc Bekoff, Frank C. Bellrose, Jr.*, Louis B. Best*, T. R. Birkhead, Charles R. Blem, Peter Boag, Walter Bock*, William R. P. Bourne, John H. Brackenbury, Richard A. Bradley*, Eliot Brenowitz, I. Lehr Brisbin*, Pierce Brodkorb*, Richard G. B. Brown*, Charles J. Burke, M. Byrd, William A. Calder, Jr.*, Thomas Caraco, Cynthia Carey*, Lynn F. Carpenter, Susan M. Case, Graeme Caughley, Mary H. Clench, Charles T. Collins*, Michael Collopy, Edward F. Connor, Peter G. Connors, Michael R. Conover*, Fred Cooke, John Cooper, Kendall W. Corbin, Richard Cowie, Joel Cracraft*, Robert B. Craig, Richard D. Crawford, John Croxall, E. Curio, Thomas W. Custer, John Davis, David DeSante, Diane De Steven, Robert W. Dickerman, James J. Dinsmore, David S. Dobkin, Richard A. Dolbeer, Hilary Dow, R. D. Drobney, William H. Drury, Alfred M. Dufty, Jr., Arthur E. Dunham, Erica H. Dunn*, Thomas J. Dwyer*, Eugene Eisenmann, Phillip F. Elliott, John T. Emlen, Robert Epting, Anthony J. Erskine, R. Michael Erwin*, P. G. H. Evans, Roger M. Evans*, David Ewert, C. J. Feare*, J. Alan Feduccia, Peter Feinsinger, Millicent Ficken*, James S. Findley, Hans Fisher, Walter Fitch, John W. Fitzpatrick*, Brian K. Follett, Eric D. Forsman*, W. J. Francis, Leigh Fredrickson, Herbert Friedmann, Carl Gans, C. Lee Gass*, A. J. Gaston, Sidney A. Gauthreaux, W. George, Frank B. Gill*, Robert E. Gill, P. D. Gingerich, Bradley M. Gottfried, Gilbert Gottlieb, Walter D. Graul, Russell Greenberg, Paul J. Greenwood, T. C. Grubb, Jr., Joseph A. Grzybowski, Svein Haftorn, Caldwell D. Hahn, F. Reed Hainsworth, William J. Hamilton, III, M. P. Harris, Richard J. Harris, Jeremy J. Hatch, Helen Hays, Robert E. Hegner, Dennis Heinemann*, Carl W. Helms*, Charles J. Henny*, Wayne Hoffman*, A. J. Hogan-Warburg, Richard T. Holmes, Dominique G. Homberger, John L. Hoogland*, Henry F. Howe*, Donald F. Hoyt*, John P. Hubbard, George L. Hunt, Jr.*, R. Hutton, Jerome A. Jackson*, Frances C. James*, Daniel H. Janzen*, Olli Järvinen*, Joseph R. Jehl, Jr.*, Paul A. Johnsgard*, Douglas H. Johnson*, David W. Johnston, Richard F. Johnston*, James R. Karr*, Janet Kear, J. Allen Keast, Bretton W. Kent, Paul Kerlinger, Lloyd F. Kiff, Lawrence Kilham, James R. King*, Warren B. King, Erwin E. Klaas*, Richard W. Knapton, Carl E. Korschgen, Gary Krapu*, John R. Krebs,Donald E. Kroodsma, James A. Kushlan, Mary K. LeCroy, Louis Lefebvre, Ross Lein*, Robert E. Lemon*, K. Lessells, J. David Ligon*, C. D. Littlefield*, Clare S. Lloyd, William J. Mader, Chris Marsh, Carl D. Marti*, Dennis J. Martin, Elden W. Martin, L. D. Martin*, Steven Martindale, Barbara W. Massey, Harold F. Mayfield*, Donald A. McCrimmon, Jr., Christopher McGowan, Judith W. McIntyre, Ann McNabb, A. H. Meier, Charles Meslow, L. Richard Mewaldt, David Miller*, Don E. Miller*, Douglas W.

(continued on p. 315)