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PERSPECTIVES IN ORNITHOLOGY

FLIGHT CALLS AND THEIR VALUE FOR FUTURE ORNITHOLOGICAL STUDIES AND CONSERVATION RESEARCH

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MANY PASSERINE BIRDS and their relatives utter flight calls, species-specific vocalizations given primarily during sustained flight, especially during migration. References to flight calls appeared in the ornithological literature as early as the 1890s, but some of the most basic features of these calls remain poorly known, including their functions, origins, ontogeny, distances over which they are used, and how much individual variation exists in the characters of the calls and their rates. With improved knowledge of these vocalizations, flight calls possibly will have a variety of applications. Identifying their function could illuminate how birds refine migration strategies during crucial decision-making periods. Because flight calls are relatively simple vocalizations, compared with many others that birds use, they provide useful characters for future evolutionary and comparative analyses. Monitoring flight calls can be a powerful method for studying nocturnal migration. However, such applications require more detailed knowledge of flight-calling behavior. Here, I summarize the available information on flight calls and highlight areas where future research may improve and expand this knowledge.

FLIGHT CALLS AND SPECIES THAT UTTER THEM

Flight calls of passerines, as well as cuckoos and woodpeckers, among others, are defined as species-specific notes, either frequency-modulated or pure, of up to several syllables that generally are in the 1–9 kHz frequency band and 50–300 ms in duration. Spectrograms of representative passerine flight calls are shown in Figure 1. These calls are the primary vocalizations given by many species of birds during long, sustained flights, particularly migratory flights (Evans and O'Brien 2002). Despite the name "flight" call, birds may produce these calls in several contexts other than migration, including while perched (notably the cardueline finches; Munding 1970) and while interacting with fledged young (notably parulid warblers; A. Farnsworth pers. observ.). Many species also utter flight calls year-round (Evans and O'Brien 2002), and some regularly give them while flying during the day (e.g. Yellow-rumped Warbler [*Dendroica coronata*]; Evans and O'Brien 2002). Flight calls are distinct from songs and, more importantly, they are distinct from other types of short calls, such as "chip" notes and alarm calls.

Nearctic and Neotropical species.—Flight calls have been studied most intensively in North America, and Evans and O'Brien (2002) compiled a guide to the flight calls of migratory birds that

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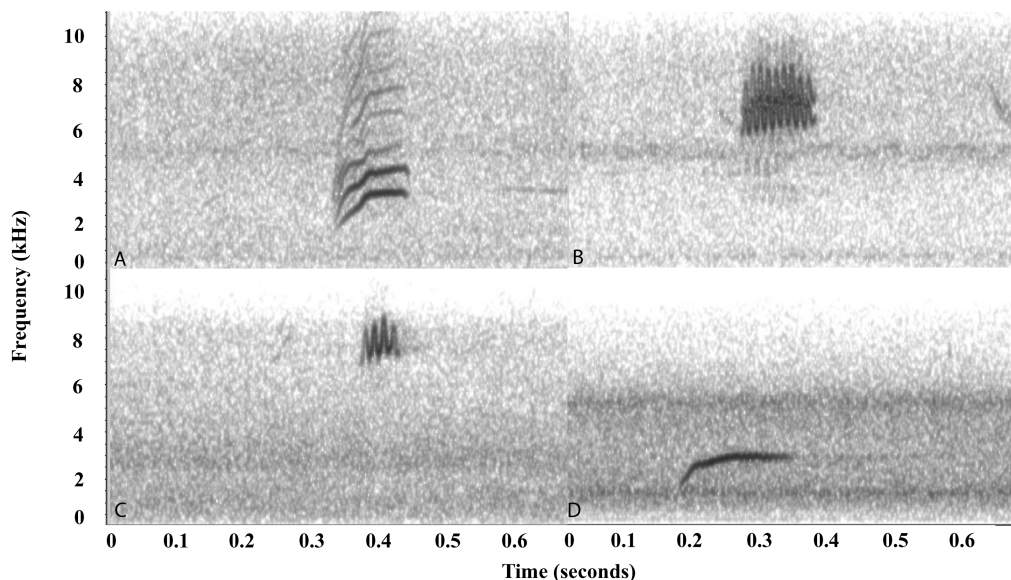


FIG. 1. Examples of passerine flight calls (from Evans and O'Brien 2002): (A) Bobolink (*Dolichonyx oryzivorus*), (B) Indigo Bunting (*Passerine cyanea*), (C) Blackpoll Warbler (*Dendroica striata*), and (D) Swainson's Thrush (*Catharus ustulatus*). Note that the axes of these spectrograms have identical scales, which facilitates comparing the different species' calls. (B) and (C) depict modulated calls, whereas (A) and (D) depict flight calls or parts of flight calls with pure tones.

occur in the eastern part of the continent, mostly east of the 100th meridian. This unique resource provides detailed information on flight calls, including descriptions of the vocalizations and calling behavior, spectrographic representations, examples, and identification tips. Not all of the species contained in the guide regularly give flight calls, and not all of those that regularly give flight calls utter them at night (these are primarily diurnal migrants). Groups of species that do not regularly give flight calls when moving during day or night include New World flycatchers (Tyrannidae), vireos (Vireonidae), and mimids (Mimidae).

Palaearctic and Palearctic species.—Although less intensively studied than Nearctic species, numerous Palaearctic and Palearctic species also utter flight calls (Chappuis 1989, van den Berg et al. 2003). Some of these are closely related to vocal New World species, such as

Turdus thrushes (e.g. Fieldfare [*Turdus pilaris*]; Redwing [*T. iliacus*]), cardueline finches, pipits, and *Regulus* crests; other species are more typically Old World, such as bee-eaters (Meropidae), *Emberiza* buntings (e.g. Rustic Bunting [*Emberiza rustica*], Ortolan Bunting [*E. hortulana*]), many wagtails (Motacillidae), larks (Alaudidae), and fringillids. Like some Nearctic birds, not all those species regularly vocalize at night. In fact, it is primarily European *Turdus* thrushes (Siivonen 1936; Browne 1953; Vleugel 1954, 1960; Chappuis 1989; van den Berg 2003) and some *Emberiza* buntings and *Regulus* crests (M. Robb pers. comm.) that regularly give flight calls during nocturnal migration. Other Palaearctic–Palearctic species also give flight calls at night, including several species of pitta (Fairy Pitta [*Pitta nympha*], S. Lin pers. comm.; Blue-winged Pitta [*P. moluccensis*], P. Round pers. comm.), some Asian and Australo-Papuan cuckoos such as Long-tailed Koel (*Eudynamis taitensis*) and Pied Cuckoo (*Clamator jacobinus*) (N. Olliver pers. comm.), and Woodland Kingfisher (*Halcyon senegalensis*) (D. Mostert pers. comm.). Research in Africa, Asia, and Australia will probably identify

numerous additional species that utter flight calls at night.

Like New World exceptions that rarely give flight calls, there are also Palearctic species that rarely give flight calls: Old World flycatchers (Muscicapidae) and Old World warblers (Sylviidae) are generally silent during migration. However, Pied Flycatchers (*Ficedula hypoleuca*) and Spotted Flycatchers (*Muscicapa striata*), which are not normally heard during nocturnal movements, apparently vocalize when visibility is poor (B. Bruderer pers. comm.; see Herremans 1993), and some sylviid warblers infrequently vocalize (similar to fledgling calls) during daytime movements (Blackcap [*Sylvia atricapilla*] and Chiffchaff [*Phylloscopus collybita*], M. Herremans pers. comm.; River Warbler [*Locustella fluviatilis*], J. Kriek pers. comm.).

Identification.—How are calling birds identified when they are migrating at night and not visible? Identification of some calls is simple, because the nocturnal vocalizations are the same as the diurnal ones (*Catharus* spp.; Howes 1912, Evans 1994). However, identification of many species is often more complicated and requires additional information, which generally comes from two distinct sources (Evans and Mellinger 1999, Evans and Rosenberg 2000): (1) Comparisons of spectrograms of diurnal flight calls of known species and unknown nocturnal flight calls—many birds observed in visible morning flights often give flight calls (Evans and Rosenberg 2000, Evans and O'Brien 2002; see Gauthreaux 1978, Hall and Bell 1981, Wiedner et al. 1992 for descriptions of the morning flight phenomenon). Also, direct comparison is possible of unknown nocturnal vocalizations and flight calls recorded from birds in captivity or from birds carrying miniature microphones (Hamilton 1962, A. Farnsworth and M. Lanzone unpubl. data, W. Cochran unpubl. data). Figure 2 shows examples of these types of comparisons. (2) Correlating the seasonal timing and geographic range of nocturnal calls with known timing and migration ranges for each species—species-specific migration calendars are available for many species and locations in North America, often generated from accounts of species killed at night in collision with television towers, lighthouses or buildings, and historical arrival and departure dates (see Evans 1994, Evans and Rosenberg 2000; see also Hedges 2001).

FLIGHT CALL RESEARCH (PRE-1959): EVIDENCE OF NOCTURNAL MIGRATION AND PATTERNS

Ornithologists debated certain aspects of bird migration strategies and patterns into the late 19th and early 20th centuries—for example, whether birds migrate across the Gulf of Mexico (Frazar 1881; Cooke 1904; Lowery 1945, 1946; Williams 1945, 1947)—but most accepted that many species migrate at night (Chapman 1888; Cooke 1904, 1915; Lowery 1946). It was largely the flight calls of migrating birds that authors cited as direct evidence of such nocturnal movements, and they used the calls to identify species, to assess the magnitude of migration, and as a quaint reminder of the wonders of bird migration. Libby (1899) tallied 3,600 calls during five hours of passive listening near Madison, Wisconsin, on 14 September 1896, the first published attempt to quantify nocturnal migration using flight calls. Kopman (1904) and Carpenter (1906) referenced thrush vocalizations heard during nocturnal migration, especially of the Veery (*Catharus fuscescens*) and Gray-cheeked Thrush (*C. minimus*), and Thayer (1903) similarly referenced the vocalizations of Black-billed Cuckoo (*Coccyzus erythrophthalmus*). Howes (1912) detailed the flight calls of Swainson's Thrush (*C. ustulatus*) in terms of location and timing of its migratory routes in autumn in the northeastern United States. Tyler (1916) highlighted the diversity of flight calls and also noted that they appear in a species' vocal repertoire during periods of migration.

Studies through the 1950s illuminated the temporal pattern of nocturnal calling (e.g. *Turdus* spp. in Finland [Siivonen 1936] and Ireland [Browne 1953], and *Catharus* spp. in the Gaspé Peninsula [Ball 1952; one of the most comprehensive studies on the timing of migration of a particular species through a region using flight calls]). Popular accounts of nocturnal call counts from eastern North America also appeared regularly, usually as call totals or interpreted numbers of *Catharus* thrushes passing over during a portion of an evening (*Audubon Field Notes*; see brief summary in Evans and O'Brien 2002).

Toward the end of the 1950s, interest in quantifying nocturnal migration sparked a new debate about the relationship between the timing of peak bird density aloft and the

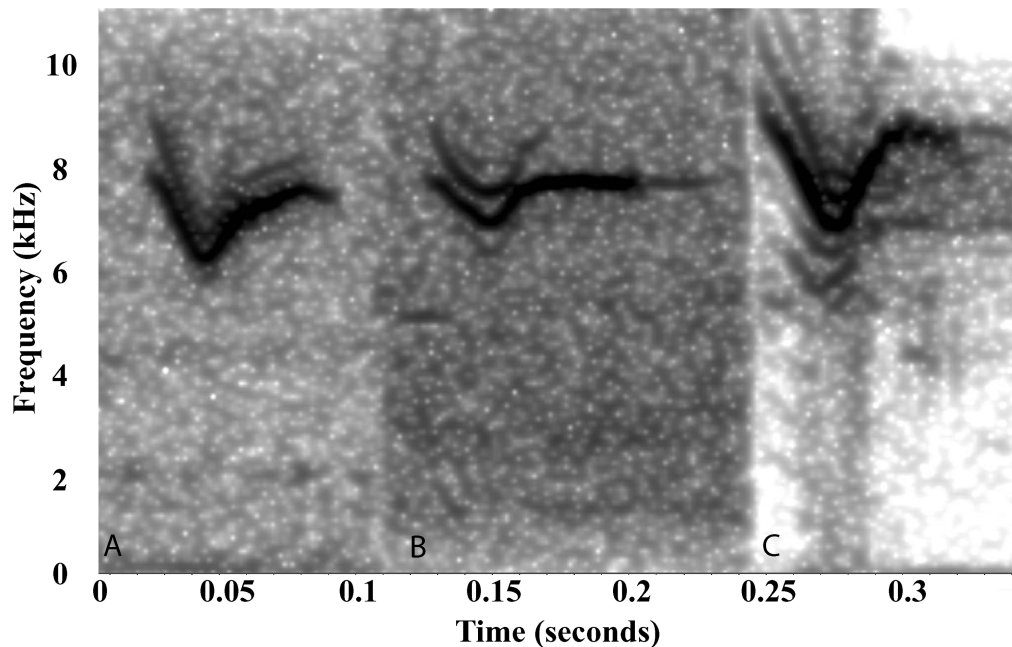


FIG. 2. Flight calls of American Redstart (*Setophaga ruticilla*): (A) diurnal flight call, (B) nocturnal flight call, and (C) flight call recorded in captivity. Note similarities among the calls, such as their basic V-shaped pattern; however, also note that calls vary individually, such as in the depth and shape of their characteristic V-pattern.

timing of peak flight-call counts. The relationship between flight-call counts and direct visual observations of migratory birds passing in front of the full moon (Lowery and Newman 1955, Newman 1956) suggested that calling peaks at a different time than the density of birds in the atmosphere: bird density peaked 2–3 hours after sunset (Lowery and Newman 1955, Newman 1956), whereas vocalizations peaked in the hours just before dawn (Ball 1952). Also, visual observations indicated that the distribution of nocturnal migrants in the air was relatively even, in contrast to flight-call data that suggested a clumped distribution (Ball 1952). To some, the record of nocturnal calling exaggerated the impression of large-scale migration detected by moon-watching (Vleugel 1960). To confound the situation further, data from European call counts indicated that calling by *Turdus* spp. peaked close to local midnight and spiked again just before dawn (Vleugel 1954, 1960). The interpretation of the acoustic record, especially in relation to actual numbers of birds aloft at night, was not at all clear.

FLIGHT CALL RESEARCH (POST-1959):

AUTOMATION, RECOGNITION, AND IDENTIFICATION

Although the limits and variability of human hearing largely prevented objective comparisons among earlier studies of migration, technological developments of the 1940s and 1950s enabled researchers to make audio recordings of nocturnal bird migration that were useful for more efficient and objective data collection, analysis, and comparisons (see Evans and O'Brien 2002). The invention of the sound spectrograph made visual comparisons of similar sounds possible (Koenig et al. 1946), and the perfection of magnetic tape and tape-recording devices made archiving of sounds a reality. Graber and Cochran (1959) sampled nocturnal flight calls using a microphone and a parabolic antenna, automatically recording calls to magnetic tape at 10-min intervals during entire nights of migration. Such techniques provided the foundation for future, in-depth examination of aural records of nocturnal migration. Graber (1968) further advanced these

techniques by comparing the acoustic record of nocturnal migration with radar and diurnal field-census data. However, the meaning of the acoustic record of nocturnal migration remained equivocal (Graber 1968), though Graber and Cochran (1959, 1960) suggested that qualitative data from acoustic monitoring complemented quantitative data from visual methods. The function of flight calls was still unknown, though Hamilton (1962) presented evidence from birds recorded in captivity that suggested that calls facilitated communication among individuals in flocks.

Although electronic technologies made acoustic sampling possible across increasingly large temporal and spatial scales of migration, labor-intensive data collection and analysis, expensive and bulky recording media, and unwieldy and often unreliable recording devices effectively limited the scope of acoustic studies. However, by the late 1980s and early 1990s, more rapid computer processing and detection algorithms (see www.oldbird.org for details) allowed researchers to resolve many technical issues that had hindered previous attempts to use acoustics to study nocturnal migration. Dierschke (1989) recorded nocturnal flight calls automatically at Helgoland, Germany, using a device activated by signals of specific duration, loudness, and frequency. This method conserved audio tape and saved analysis time, bypassing portions of the night when there was no calling. Improved detection and classification algorithms (H. G. Mills pers. comm., A. J. Taylor pers. comm.) provided the means to extract flight calls automatically from either previously made recordings or real-time data from an active microphone. This software generally detects nocturnal flight calls by locating isolated temporal energy peaks in a specified frequency range and classifies calls by tracking frequencies over time with an artificial neural network. Simultaneous advances in methods of spectrographic analysis (Clark et al. 1987) and computer software and programs (CANARY; Charif et al. 1995) enabled more rapid examination and discrimination of similar calls.

Inexpensive portable and durable microphone designs, pioneered by Evans (1994, 2000; Evans and Mellinger 1999), facilitated collection of flight-call data across larger geographic and temporal scales (Evans and Rosenberg 2000, Millikin 1998, H. G. Mills pers. comm.).

Improved radar technologies and coverage afforded the opportunity to compare measures of nocturnal migration at much greater scales (after Graber 1968; Larkin et al. 2002, Millikin 2002, Farnsworth et al. 2004). Identification of flight calls also progressed and culminated in the production of the first electronic identification guide (Evans and O'Brien 2002).

PATTERNS OF FLIGHT-CALLING BEHAVIOR

Effects of atmospheric conditions.—Several relationships between call counts and atmospheric conditions are apparent from the literature and to observers in the field during migrations. Counts of calls increase with increasing cloud cover and decreasing cloud ceiling, especially under artificial lighting (Cochran and Graber 1958, Graber and Cochran 1960, Ogden 1960, Dorka 1966, Graber 1968, Clemens 1978, Thake 1983, Evans and Mellinger 1999). Call counts also increase as birds approach boundaries between air masses of different density (Petersen 1956), where conditions unfavorable for migration—such as precipitation, high winds, and poor visibility—force birds to pile up or descend (Graber and Cochran 1960). Calling usually occurs during periods of seasonally appropriate wind directions (Graber and Cochran 1960). Vleugel (1960) found that call counts of *Turdus* in Holland during autumn increased with the passage of cold fronts and decreasing temperature. Call counts are also positively correlated with 24-h trends of falling temperatures in autumn, whereas the inverse is true in the spring (Graber and Cochran 1960). Two potential caveats exist when extrapolating from the results of these studies: the studies represent site-specific results and there is no information about rates of calling and their relationship to independent measure of bird numbers.

Effects of altitude and topography.—The effects of altitudes on calling rates are poorly known. Evans (2000) recorded many vocalizations within 500 m of the ground during autumn migration (see also Black 1997). Evans and Rosenberg (2000) and Evans (2000) indicated that flight altitudes of calling wood-warblers were less than 200–300 m those of calling thrushes (up to 450–500 m). There is also temporal variation in the altitudes of calling birds, and average altitudes may be substantially lower or higher on different nights (Black 1997, W. Evans

pers. comm.). It is not known whether calling is primarily a boundary-layer phenomenon, occurring only in the atmospheric strata close to the ground.

Although migration occurs across broad spatial scales (Lowery and Newman 1955, Parslow 1969, Gauthreaux et al. 2003), evidence suggests that topographic features such as mountains or hills and coastlines concentrate birds (Eastwood 1967; Bruderer 1978; Richardson 1978, 1990; Åkesson 1993; Williams et al. 2001); these features also appear to concentrate flight calls. Evans and Mellinger (1999) found that changes in wind conditions resulted in larger numbers of calls counted on the coast of Texas; southwesterly winds forced birds migrating inland toward the coast, and to avoid drifting over the Gulf of Mexico, these birds piled up on the coast and then moved north along it. Evans (2005) reported that when the cloud ceiling is low, altitudinal variations of terrain disrupt the flight of calling migrant passerines and effectively concentrate calling birds in areas of lower altitudes.

Temporal patterns.—Despite the variability in all these relationships, patterns of call counts across seasons and years are often consistent and probably represent some true behavioral and biological patterns (e.g. the migration timing of different species). Conversely, nightly temporal patterns of calling are much more variable. These patterns could represent site-specific differences and additional unknown behavioral and biological patterns. Ball (1952) recorded ~90% of thrush vocalizations in the hours just before dawn, with a ratio of 27 calls after midnight to 1 call before midnight (from 33,921 calls). Graber and Cochran (1960) supported this conditionally, though they detected migration consistently at any hour of the night, but a marked peak in calling occurred in the hours before dawn if migration occurred all night. Farnsworth and Russell (2005) reported a similar pattern in an acoustic study of migration over the Gulf of Mexico, finding that the nightly peak of call counts occurred in the two hours just before dawn. By contrast, call counts of *Turdus* in Europe usually peaked in the hours closest to local midnight, with deviations from this pattern usually associated with the passage of a front (Siivonen 1936; Browne 1953; Vleugel 1954, 1960). Furthermore, flight-call counts have varied extensively throughout the night,

though on many nights, peaks occurred in the hours close to local midnight (Ross et al. 1995, Farnsworth et al. 2004).

Reasons for the variability in nightly peak call counts are not known, but they might include locally varying weather conditions (Graber and Cochran 1960, Graber 1968, Evans and Mellinger 1999, Evans and Rosenberg 2000, Evans 2000) and variation in flock sizes and species composition (Marler 1956; Hamilton 1962; Thake 1981, 1983; Farnsworth et al. 2004). Some variability might result from different species descending at different times of the night and calling at different rates during descent (Graber 1968). Furthermore, rates of calling may vary highly among individuals. The hourly mean call counts for Swainson's Thrushes bearing small microphones "ranged from 0 to 37, including one individual [briefly] vocalizing 16 times minute⁻¹ and one individual that did not call for 3 hours" (W. Cochran pers. comm.).

Hemispheric patterns.—Another intriguing but unexplained pattern is that, by nearly all accounts, vocalization by nocturnally migrating birds in the Palearctic seems to exhibit a different pattern than vocalization in the Nearctic migration system. Calls are uttered more frequently, at greater magnitude, and by more species in the New World. Whether this is a function of small sample sizes in the European studies, fundamental behavioral differences between the migration systems, phylogenetic effects, or some combination thereof is unknown. Anecdotal accounts from numerous European researchers suggest that flight calling is limited even in the species that regularly vocalize at night (compare Vleugel 1960 and Ball 1952).

FUNCTION OF FLIGHT CALLS

Previous workers have suggested that birds give flight calls in response to fear (Hudson 1923), loneliness (Drost 1963), hunger, or the light of approaching dawn (Ball 1952). In some species, flight calls may signify the presence of a transient individual in a resident's territory (e.g. European Blackbird [*T. merula*]; M. Robb pers. comm.). Other anecdotes suggest that some wood-warblers use flight calls in aggressive interactions, though this association is apparently rare (A. Farnsworth pers. obs.). The monomorphic Swinhoe's Storm-Petrel (*Oceanodroma*

monorhis) utters flight calls for sex-specific discrimination in situations with limited visual information, especially at night (James and Robertson 1985, Taoka and Okumura 1990), but this is not known in passerines. The consensus from the recent literature, together with anecdotal evidence, suggests that flight calls help to maintain groups and stimulate migratory restlessness or *zugunruhe* in conspecifics, perhaps especially in inexperienced birds (Tyler 1916; Ball 1952; Hamilton 1962; Drost 1963; Graber 1968; Thake 1981, 1983). Studying captive Bobolinks (*Dolichonyx oryzivorus*), Hamilton (1962) found that calling triggered mutual responses from birds in proximity and was associated with migratory periods, nightly unrest, and increased fluttering and calling.

Flight calls also highlight differences among geographically separated populations and, at least in some species, allow recognition of individuals (Mundinger 1970, Marler and Mundinger 1975, Mundinger 1979, Adkisson 1981, Groth 1993b, Hahn et al. 2001, Sewall et al. 2004). Whether the calls of nocturnally migrating birds function in the same way is not known. Furthermore, whether birds call in a way that is similar to that of contact calls and alarm calls, for group cohesion and social affiliation, is also unknown (Mammen and Nowicki 1981; Nowicki 1983; Marzluff and Balda 1992; Groth 1993b; Dufty and Hanson 1999; Baker 2000, 2004; Hahn et al. 2001; Marler 2004; Sewall et al. 2004). Nocturnal groups may also be social, maintained by flight calls rather than contact and alarm calls (Lowery and Newman 1955; Graber and Cochran 1960; Hamilton 1962, 1967; Gauthreaux 1972; Balcomb 1977). Interspecific grouping indeed occurs during nocturnal migration (Graber and Cochran 1960, Hamilton 1962, Evans and Mellinger 1999, Evans and Rosenberg 2000); however, concentrations may be random or result from small-scale atmospheric motion that could promote such structure (Larkin 1982).

Although Balcomb (1977) argued against the benefits of coordinated migrant groups for nocturnal orientation, migrating birds may use flight calls for orientation, to reduce dispersion of headings, and to detect changing wind direction by echolocation and monitoring Doppler shifts (Lowery and Newman 1955; Griffin 1969; Griffin and Buchler 1978; Larkin 1978; Thake 1981, 1983). Such functions could be especially

useful when visibility is reduced, increasing the likelihood of being heard, hearing others, and avoiding collisions (Graber 1968, D'Arms and Griffin 1972, Thake 1983, Larom et al. 1997). This could be particularly important for inexperienced migrants; indeed, evidence suggests that young birds vocalize more frequently than adults (W. Cochran pers. comm.). Many flight calls exhibit a pattern of rapid frequency sweeps that may be advantageous for birds deriving information (*contra* Thake 1983), with some frequencies encountering complex and favorable interference patterns for sound reflection or retransmission (Griffin and Buchler 1978). The ability to locate calls of other individuals improves as a function of abrupt beginnings and endings, discontinuities, and repetition (Hamilton 1962), which also characterize many flight calls. Indeed, birds can resolve small changes in frequency (e.g. Rock Pigeon [*Columba livia*], Quine 1978; Budgerigar [*Melopsittacus undulatus*], Dooling and Saunders 1975, Park and Dooling 1985, Brown et al. 1988, Ali et al. 1993; and Barn Owl [*Tyto alba*], Quine and Konishi 1974).

FUTURE DIRECTIONS

There are major gaps in our understanding of flight-calling behavior. To understand its functional significance, we need to explore its causes, ontogenetic aspects, evolutionary history, and patterns of change over time (Tinbergen 1963).

Are flight calls learned?—Although flight calls are one of the earliest calls to appear in the repertoire of juvenile cardueline finches (Mundinger 1979), these species learn and change these calls by imitation throughout life (Mundinger 1970). Is this pattern found in other passerines? Hamilton (1962) suggested that the calls were innate. Comparing the flight calls of captive-bred birds with diurnal and nocturnal vocalizations of wild birds could provide some answers. No detailed seasonal usage pattern of flight calls is available, and developing a timetable for many species should be informative. Understanding the ontogeny of flight calls is crucial for attempts to classify them and has important implications for determining their functions. Furthermore, if flight calls are learned in a diverse array of passerines, the influence of vegetation structure and ambient noise spectra

may play an important role in their development (Hansen 1979, Nottebohm 1985).

What factors constrain flight calls?—Recent studies show that different species of birds have different detection thresholds for signals in ambient noise (Klump 1996, Langemann et al. 1998), as well as different hearing thresholds (Dooling and Saunders 1975, Dooling 1982, Okanoya and Dooling 1987). Differences in the perceptual abilities of species could play important roles in determining variation in call frequencies. Flight calls may also be subject to different selection pressures related to encoding information (relative to selective pressure on songs). Reverberation, amplitude modulation rate, consistency of transmission, and spectral distribution of ambient noise are important sonic properties that define vocalizations, and these properties vary with selection pressures among habitats (Marler 1955, Morton 1975, Ryan and Brenowitz 1985, Wiley 1991). How these properties relate to the use and function of flight calls is not known. Also, although Hamilton (1962) did not believe that predators play a major role in shaping flight calls, Gill and Sealy (2003, 2004) found evidence that high-frequency *seet* calls alert individuals to brood parasites. Flight calls, which have similarly high frequencies and short durations, may be used to communicate information above the frequency thresholds of predators (Langemann et al. 1998). If these calls are related in some way to fledgling vocalizations (see Tyler 1916), there may be a direct relationship between such anti-predatory behaviors and flight calls.

Over what distances are flight calls used?—No one has studied the range of distances over which birds communicate through flight calls. Because the frequencies of signals indicative of long-range communication are lower (Marten and Marler 1977, Larom et al. 1997, Larom 2002), the characteristically high frequencies of these calls suggest that they may be used primarily for communication over short distances. However, the constraints associated with sound production during flight are not known, though they have implications for nocturnal communication and the architecture of nocturnal groupings. Furthermore, optimal in-flight communication using certain frequencies could shape flight vocalizations that either travel best in specific atmospheric and microclimatic strata or avoid specific ambient noise spectra (Larom

2002, Rundus and Hart 2002, Slabbekoorn et al. 2002, Slabbekoorn and Peet 2003).

How variable are flight-call characters?—Intraspecific variation in flight calls is not a recent discovery (Ball 1952), but the extent of this variation in call characters, such as frequency, has only recently received greater attention (Hahn et al. 2001, Evans and O'Brien 2002, Sewall et al. 2004). Evidence suggests that the characteristics of certain species' flight calls, notably those of thrushes, larks, pipits, and finches, vary substantially (Evans and O'Brien 2002, M. Robb pers. comm., W. Cochran unpubl. data). The implications of such variation are also unknown, though Munding (1970, 1979) suggested that call-matching and imitation could be important. A few studies have explored the extent of phylogenetic signals in songs (e.g. kinglets; Päckert et al. 2003) and calls (e.g. herons; McCracken and Sheldon 1997), but few species are represented, and none of these studies explicitly addressed flight calls. Similarly, if character release exists in flight calls, the relationship between it and the diversity of related species is not known.

Are there potential applications for flight calls?—Flight calls may be useful characters for comparative analyses among taxa (Munding 1979, Farnsworth and Lovette 2005), aiding in resolving cryptic species (Groth 1988) and delineating taxa (Munding 1979; Adkisson 1981; Groth 1988, 1993a; Hahn et al. 2001; Sewall et al. 2004). However, categorizing natural variation in flight calls and expanding the sampling of spatial and temporal distributions of flight-call data sets are critical precursors to pursuing such directions (Sewall et al. 2004). Flight calls may also shed light on habitat preference and morphology (Groth 1993a, b). For example, in phylogenetically controlled and uncontrolled analyses, Farnsworth and Lovette (2005) found little support for morphological constraints on flight-call frequencies in parulids. This pattern differs from the widely reported pattern in larger birds that vocalize at lower frequencies (Greenewalt 1968, Wallschläger 1980). There are also diverse and potentially powerful applications for monitoring flight calls to document broad front patterns of species-specific nocturnal movements and altitudinal distribution of calling migrants (Tyler 1916; Ball 1952; Graber and Cochran 1960; Graber 1968; Evans 1994, 2000; Evans and Mellinger 1999; Evans and Rosenberg 2000) and to identify

the points of origin of calling migrants (W. Evans pers. comm.).

Patterns of nocturnal bird migration as detected by radar and acoustic methods do not always differ, though these methods illuminate what are likely fundamental differences in patterns of behaviors (Ross et al. 1995, Larkin et al. 2002, Farnsworth et al. 2004). Nocturnal call counts of migrating birds can be useful as indices of nocturnal bird density aloft (Larkin et al. 2002, Farnsworth et al. 2004), though extensive variation in calling rates (within and among species) poses a major challenge for measuring bird density from flight calls alone (Libby 1899, Graber 1968, Dierschke 1989, Evans and Mellinger 1999, Farnsworth 2001, Farnsworth et al. 2004). Moreover, there can be substantial differences between a high volume of migration and high incidences of calling (Graber and Cochran 1960, Ross et al. 1995, Farnsworth et al. 2004). More detailed studies of nocturnal migration using radar and acoustic methods simultaneously, and studies that span even larger spatial and temporal scales, will be necessary to resolve these issues. More studies using stand-alone methods based on flight-call counts will generate a base of departure and arrival data as well as relative proportions of species on different nights.

CONCLUDING REMARKS

Many additional questions remain unanswered, and future studies of flight calls will clearly be challenging; however, they also will provide excellent opportunities to improve our understanding of avian migration and life histories and the way these relate to such a variable behavior. Why are some species silent during nocturnal migration? Is the regular use of flight calls related to other behavioral traits, such as flock foraging? Do birds migrating in similar directions at similar times of year show convergent vocalizations (Hamilton 1962, 1967; Graber 1968; Thake 1981, 1983)? Do birds benefit from reciprocal calling by enhancing associations with conspecifics and, after landing, by reducing predation risk on the ground (see Hamilton 1971)? There are numerous applications for flight calls in applied conservation, ecological, behavioral, and evolutionary studies. Intraspecific variation in flight-calling behavior could be the result of proximate factors on a

migratory route (e.g. flying in changing weather conditions or approaching ecological barriers), whereas interspecific variation in flight-calling behavior is possibly the result of ultimate factors (evolution of migratory strategies, differences in foraging strategies). Regardless of the hypotheses or the applications, it must be remembered that the interpretation of flight-call counts or calling behavior could be greatly misleading without consideration of such underlying behavioral information (Graber 1968, Evans and Mellinger 1999).

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