Ornithology, 2023, 140, 1–21
https://doi.org/10.1093/ornithology/ukad021
Advance access publication 17 May 2023
Research Article

AMERICAN ORNITHOLOGICAL SOCIETY
Ornithology
OXFORD

The adaptive significance of off-lek sociality in birds: A synthetic review, with evidence for the reproductive benefits hypothesis in Long-wattled Umbrellabirds

H. Luke Anderson,[1,2,*] Jorge Olivo,[2] and Jordan Karubian[1,2]

[1]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana, USA
[2]Fundación para la Conservación de los Andes Tropicales, Quito, Ecuador

*Corresponding author: handerson@tulane.edu

ABSTRACT

Anecdotal evidence suggests that lekking birds exhibit considerable variation in form and degree of sociality away from the lek, yet this phenomenon has received very little theoretical or empirical research attention. Here, we provide the first synthetic literature review of off-lek sociality in birds and develop a conceptual framework for the potential adaptive function of off-lek sociality across lekking taxa. We then present a case study of the Long-wattled Umbrellabird (*Cephalopterus penduliger*), where we find support for the hypothesis that off-lek sociality is primarily driven by male reproductive incentives for coordinating lek attendance during the breeding season. During periods of high lekking activity, male umbrellabirds depart the lek in highly coordinated groups and maintain larger off-lek social groups relative to periods of low lekking activity. These seasonal differences in off-lek sociality do not occur in females, are not explained by patterns of foraging behavior, and are expected to confer individual-level benefits for participating males. Both the literature review and empirical study of umbrellabirds suggest that off-lek interactions and behavioral strategies may shape sexual selection processes at leks in important ways. Further research into this historically understudied area of lekking species' behavioral ecology will likely deepen our understanding of the evolutionary dynamics of lek mating.

Keywords: *Cephalopterus penduliger*, group foraging, lek mating, literature review, off-lek sociality, Pipridae, sexual selection

How to Cite

Anderson, H. L., J. Olivo, and J. Karubian (2023). The adaptive significance of off-lek sociality in birds: a synthetic review, with evidence for the reproductive benefits hypothesis in Long-wattled Umbrellabirds. Ornithology 140:ukad021.

LAY SUMMARY

- Social behavior away from the lek may influence and interact with sexual selection processes in important ways, yet this component of lekking species' behavioral ecology remains very poorly known.
- A synthetic literature review suggests considerable diversity in the form and degree of off-lek sociality among lekking birds, both within and between species.
- Potential adaptive explanations for the function of off-lek sociality in a given species include foraging enhancement, predation avoidance, and mating benefits.
- In Long-wattled Umbrellabirds, we find that the size and coordination of male off-lek groups increases during the mating season. This pattern is not observed in females and is not related to the proportion of fruit in the diet.
- We suggest that off-lek sociality in umbrellabirds enables males to synchronize foraging and display periods, which is expected to confer individual-level reproductive benefits.

La importancia adaptativa de la sociabilidad fuera del lek: una revisión sintetizada, con evidencia por la hipótesis de los beneficios reproductivos en el Pájaro Paraguas Longipéndulo

RESUMEN

Evidencia anecdótica sugiere que las aves que forman leks exhiben variación considerable en la forma y el grado de sociabilidad fuera del lek, pero este fenómeno ha recibido poca atención teórica o empírica. Aquí, presentamos la primera revisión sintetizada de la literatura sobre la sociabilidad fuera del lek en aves y desarrollamos una estructura conceptual para la función adaptativa potencial de la sociabilidad fuera del lek en taxones que forman leks. Luego, presentamos un estudio de caso del Pájaro Paraguas Longipéndulo (*Cephalopterus penduliger*), en donde encontramos sustento para la hipótesis que la sociabilidad fuera del lek es impulsada principalmente por incentivos reproductivos de los machos para coordinar la asistencia al lek durante la temporada de reproducción. Durante períodos de alta actividad en los leks, los machos se alejan del lek en grupos altamente coordinados y mantienen grupos sociales más grandes fuera del lek en relación con los períodos de baja

Submission Date: December 12, 2022. Editorial Acceptance Date: April 8, 2023

actividad en los leks. Estas diferencias estacionales en la sociabilidad fuera del lek no ocurren en las hembras, no se explican por patrones de comportamiento de forrajeo, y se espera que otorguen beneficios a nivel individual para los machos participantes. Tanto la revisión de la literatura como los estudios empíricos del Pájaro Paraguas Longipéndulo sugieren que las interacciones fuera del lek y las estrategias de comportamiento pueden influir de manera importante en los procesos de selección sexual en los leks. Investigaciones adicionales en esta área históricamente poco estudiada de la ecología del comportamiento de las especies que forman leks probablemente profundizarán nuestra compresión de las dinámicas evolutivas de los sistemas de apareamiento en lek.

Palabras clave: apareamiento en lek, *Cephalopterus penduliger*, forrajeo social, Pipridae, selección sexual, sociabilidad fuera del lek, revisión literatura

INTRODUCTION

Taxonomically diverse organisms including insects, fish, amphibians, mammals, and birds form leks (Höglund and Alatalo 1995), where females visit aggregations of displaying males solely to assess mates and copulate (Bradbury 1981, Wiley 1991). Lek mating systems are generally characterized by polygyny, high male reproductive skew, and a lack of male parental care (Kirkpatrick and Ryan 1991, Mackenzie et al. 1995). These conditions, along with the relative logistical ease of data collection at lek sites, have enabled a series of groundbreaking theoretical and empirical advances in our understanding of mate choice and sexual selection (Andersson 1994, McDonald and Potts 1994, Höglund and Alatalo 1995, Rowe and Houle 1996, Kokko et al. 1999, DuVal and Kempenaers, 2008). However, in striking contrast to the extensive research on dynamics at leks, very little is known about behavior away from the lek for the vast majority of lekking organisms. In birds, a group in which lekking has evolved independently in at least 14 families (Höglund and Alatalo 1995), the ecological and evolutionary causes and consequences of off-lek social behavior merit further study: not only does time away from the lek comprise a major portion of the natural history of these organisms, but off-lek behavioral strategies may have important consequences for individual fitness, including indirect effects on reproductive outcomes at the lek.

Recognizing that multiple factors likely interact to shape the form and degree of off-lek sociality in a given species, we identify 4, non-mutually exclusive hypotheses for the adaptive significance of off-lek sociality (see Table 1). First, as in non-lekking animals, sociality away from the lek may be influenced by selective pressures related to predation. Off-lek group formation may reduce predation risk via collective vigilance, predator confusion, dilution effects, or reducing encounter rates (hereafter, the "antipredator hypothesis") (Buskirk 1976, Foster and Treherne 1981, Pulliam and Millikan 1982, Landeau and Terborgh 1986, Ioannou et al. 2011). Generally, species facing greater predation risk may be expected to exhibit greater sociality away from the lek, with sociality increasing survival for participating individuals. Depending on the degree to which sexually dimorphic traits (e.g., body size, handicapping or conspicuous ornaments) influence predation risk, males and females may also be expected to exhibit varying degrees of off-lek sociality.

Second, sociality away from the lek may enable organisms to more efficiently find and exploit food sources (hereafter, the "resource acquisition hypothesis"). Social foraging may be especially important for species feeding on ephemeral, patchily distributed, and locally abundant resources (Krebs et al. 1972, Thompson et al. 1974, Pulliam and Millikan 1982, Egert-Berg et al. 2018), as is the case for many frugivorous lekking birds (Beehler and Pruett-Jones 1983). If social foraging is driven by the acquisition of patchy resources such as fruit, then the degree of off-lek sociality may correspond with the relative importance of fruit as a dietary component, seasonal variation in the abundance or patchiness of fruit on the landscape, or both (Clark and Mangel 1984). Moreover, if the lek acts as a foraging information center where individuals obtain information about the location of such resources (Ryder et al. 2006, Tori et al. 2008), departures from the lek would be expected to occur in a coordinated manner to increase the cohesion of a foraging party or enable less successful individuals to follow more successful individuals to high-quality foraging localities (Ward and Zahavi 2008).

A third possibility is that off-lek sociality does not serve a function per se, but rather arises as an incidental byproduct of individuals exploiting shared resources (hereafter, the "incidental aggregation hypothesis"), as has been proposed to explain aggregations at fruiting trees and bathing sites (Lill 1974b, Théry 1992, Jullien and Thiollay 1998). If off-lek group formation is driven primarily by incidental aggregation, then sociality should be greatest when individuals are actively using a shared resource. Furthermore, if aggregation at shared resources is non-adaptive and there is no selective benefit to coordinating off-lek feeding periods, individuals should depart from the lek in an uncoordinated, sporadic manner.

A fourth, and currently underappreciated, possibility is that off-lek sociality confers reproductive benefits to lekking males. Maintaining cohesive social groups at all stages of a foraging bout—leaving the lek, foraging away from the lek, and returning to the lek—may allow males to synchronize foraging and display periods, thereby facilitating larger effective lek sizes (i.e., more males displaying concurrently) in a way that would not be possible if individuals foraged independently. Such coordination of lek attendance has the potential to provide fitness benefits for individual males because larger leks often experience higher visitation and copulation rates per capita (Alatalo et al. 1992, Lank and Smith 1992, Höglund et al. 1993). In addition, males at a lek may benefit from monitoring, matching, or cooperating with the display activities of their rivals or kin (Shorey et al. 2000, Cestari et al. 2016, Shogren and Boyle, 2021), providing additional incentives for synchronizing movements to and from the lek independent of lek-size advantages. Based on the expected benefits of attending the lek with other males, this hypothesis for the function of off-lek sociality (hereafter, the "reproductive benefits hypothesis") predicts coordinated male movements to and from the lek, greater male off-lek sociality during the mating season compared to the non-mating season, and—all else equal—greater off-lek sociality in males than in females.

To improve our understanding of off-lek sociality, we first compile published information about off-lek behavior in lekking birds, as a comprehensive review has not been conducted to date. We then leverage a long-term observational dataset to gain insight into the form and potential adaptive significance of off-lek sociality in a species of lek-mating frugivore, the Long-wattled Umbrellabird (*Cephalopterus*

TABLE 1. Conceptual and hypothesis-testing framework. Hypothesized drivers of off-lek sociality, associated rationale and predictions, and results of the umbrellabird case study.

Hypothesis	Rationale	Predictions	Supported in umbrellabirds?
1. Reproductive benefits	Maintaining off-lek social groups may enable lekking males to coordinate foraging and display periods. Such co-ordination should result in greater concurrent lek attendance, which in turn is expected to benefit most males by increasing female visitation rates and reducing mating skew.	1a. Males will depart the lek in coordinated groups, and departures will be more coordinated during high-lekking periods.	Yes
		1b. Males will exhibit greater off-lek sociality during high-lekking periods than low-lekking periods.	Yes
		1c. Males will exhibit greater off-lek sociality than females during high-lekking periods.	Yes
		1d. Males will return to the lek in a coordinated manner during high-lekking periods.	Yes [a]
		1e. Per-capita visitation and copulation rates will be higher at leks where males coordinate attendance via cohesive off-lek sociality.	NA [b]
2. Resource acquisition	Off-lek sociality may facilitate exploitation of patchy or ephemeral resources. In frugivorous species, one or both sexes may be expected to forage socially to maximize foraging efficiency or success.	2a. Males (and, if present, females) will depart the lek in coordinated groups.	Yes
		2b. Males will exhibit greater off-lek sociality when the diet is primarily composed of fruit.	No
		2c. Females will exhibit greater off-lek sociality when the diet is primarily composed of fruit.	No
		2d. Both sexes will exhibit greater social foraging when resources are patchier or scarcer on the landscape.	NA [b]
		2e. Foraging success and/or efficiency will correlate positively with group size.	NA [b]
		2f. Species that forage on ephemeral, patchy, and locally abundant resources will exhibit greater off-lek sociality than species that do not.	NA [b]
3. Predator avoidance[c]	Group formation can reduce individual predation risk via increased vigilance, dilution effects, or confusion effects.	3a. If body size is a major determinant to predation risk, females will exhibit greater off-lek sociality than males due to their smaller size.	No
		3b. If conspicuousness or maneuverability are major determinants of predation risk, males in species with male-biased ornamentation will exhibit greater off-lek sociality than females due to their handicapping ornaments and/or conspicuous coloration.	Yes [c]
		3c. Within species, group size will correlate negatively with predation rate.	NA [b]
		3d. Between species, degree of sociality will correlate positively with predation risk.	NA [b]
4. Incidental aggregation	Social group formation may be non-adaptive and result from incidental aggregations at shared resources (e.g., fruiting trees, bathing sites).	4a. Males will depart the lek in a sporadic, uncoordinated manner.	No
		4b. Off-lek group sizes will be larger when birds are congregating at a shared resource (e.g., actively foraging at a fruiting tree).	No

[a]Prediction was supported by anecdotal observations during the study period.
[b]Prediction could not be assessed with the current data.
[c]Due to a lack of known predators, this hypothesis is unlikely to apply to umbrellabirds.

penduliger). Specifically, we provide an empirical evaluation of the non-mutually exclusive hypotheses that off-lek sociality (1) enables males to coordinate lek attendance (the reproductive benefits hypothesis); (2) aids either sex in exploiting patchily distributed fruit resources (the resource acquisition hypothesis); or (3) serves no adaptive function (the incidental aggregation hypothesis). Our data did not allow us to directly test the antipredator hypothesis, although we consider it unlikely in the umbrellabird system due to the lack of known natural predators of adults (Snow 1982). We tested the associated predictions of these hypotheses (Table 1) using data on umbrellabird foraging behavior, lekking activity, and off-lek sociality collected over a 16-year period in northwestern Ecuador.

METHODS

Literature Review

We conducted an extensive review of the peer-reviewed literature to aggregate published information about lekking species' sociality in off-lek and non-mating contexts. We first compiled all species for which lekking behavior is reported in Beehler and Pruett-Jones (1983), Cohn-Haft et al. (1997), Drovetski et al. (2006), Kirwan and Green (2011), Billerman et al. (2020), and Bretagnolle et al. (2022), omitting species for which lekking behavior was unconfirmed. We next extracted available information about a species' off-lek or non-breeding sociality from these sources as available (e.g., in species accounts). To obtain additional information, we also queried Web of Science and Google Scholar for relevant keywords ("off-lek," "off lek," "off leks," "non-lek," "away from the lek," "away from leks," "away from lek sites"), followed citations in these papers to locate additional relevant sources, and searched for individual lekking species by name and relevant terms ("sociality," "groups," "flocks," and the aforementioned keywords). For the purposes of this review, we defined off-lek sociality as social behaviors occurring away from the lek, during the non-breeding season, or during foraging (see Table 2). We adhered to definitions of sociality that consider only within-species associations (e.g., Tinbergen 1951, Wilson 1975) and thus did not include heterospecific interactions or mixed-species flocking in our literature review. Lekking species for which no off-lek sociality information was available were excluded.

We recognized the following categories of off-lek sociality: solitary (individual occurring alone), pairs (2 birds of opposite or unspecified sex), all-male groups (2 or more males), all-female groups (2 or more females), mixed-sex groups (groups of 3 or more containing both adult males and females), juvenile male groups (2 or more juvenile males), and unspecified conspecific groups (groups of 3 or more for which age or sex composition was not reported). Because females in lek mating systems generally nest away from the lek and conduct all parental duties alone, we assumed this form of solitary behavior to be universal across lekking species and did not report it in the context of this review.

Finally, to visualize evolutionary patterns in off-lek sociality, we overlaid the types of sociality observed in manakins (Pipridae)—a well-studied family of Neotropical lekking birds for which information was available about a large number of species ($n = 25$)—on a recently published and well-resolved phylogeny for the clade (Leite et al. 2021). We generated a reduced version of the manakin phylogeny (i.e., including only species for which off-lek sociality information was available) using the *APE* package in *R* (Paradis et al. 2004). Rather than serving as a rigorous phylogenetic analysis of the trajectory of off-lek sociality evolution in the family, this representation is intended to depict the current state of knowledge in a well-studied avian group and illuminate patterns of diversity to stimulate further research.

Case Study in Umbrellabirds

Study system.

We evaluated our hypotheses in the Long-wattled Umbrellabird. Long-wattled Umbrellabirds (hereafter, "umbrellabirds") are large-bodied frugivores endemic to the Chocó Biogeographic Region (Snow 1982), a biodiversity hotspot and area of conservation concern spanning western Colombia and Ecuador (Myers et al. 2000). Due primarily to habitat loss from deforestation, the species is considered *Vulnerable* to extinction (BirdLife International 2020). Umbrellabirds are characterized by pronounced sexual dimorphism, with males exhibiting greater body size, larger crests, and tremendously long wattles used in courtship displays (Berg et al. 2000, Tori et al. 2008, Karubian and Durães 2014). Males form exploded leks (~1 ha in area) comprising 5–15 individuals. Display territories are small (~25 m^2), and calling and display behavior typically occurs from a single canopy-level perch. Most males hold a long-term display territory at a single lek, although some "floater" males move itinerantly between leks without holding a fixed territory (Karubian et al. 2012). The highest display activity occurs in the early mornings and late afternoons between August and February (i.e., the "high-lekking season"), although low levels of lekking activity persist between March and July (i.e., the "low-lekking season") (Karubian et al. 2012, Karubian and Durães 2014). Both sexes are highly frugivorous and serve as important seed-dispersal agents for over 30 plant species in the Chocó (Karubian and Durães 2014). The species also reportedly consumes insects, and females provision nestlings with insects and small vertebrates (Karubian et al. 2003, Greeney et al. 2012). Anecdotally, male umbrellabirds have been observed departing and returning to the lek in a coordinated manner and foraging in groups (Tori et al. 2008), whereas females tend to be more solitary (Karubian et al. 2012).

Data collection.

We continuously gathered data on umbrellabird lekking and foraging behavior from October 2002 to August 2018 as part of a long-term study in and around the Bilsa Biological Station (BBS; 79°45′W, 0°22′N; 330–730 m elevation) in northwestern Ecuador. BBS is a 3,500-ha reserve consisting of contiguous forest of varying age and degree of past disturbance, and the site is surrounded by an increasingly deforested agricultural landscape.

To monitor activity at lek sites, we arrived at a given lek prior to the start of morning activity (0530 hours) and conducted a standardized 15-min survey beginning immediately after the first song ($n = 800$ surveys between 2002 and 2018). During surveys, we stood at the geographic center of a given lek and estimated the total number of displaying males attending the lek by noting the location of each call. Between 2004 and 2007, we sporadically remained at the lek on some mornings until ~0700 hours to record the composition and size of umbrellabird groups departing the lek. Sampling effort was equivalent year-round, and similar numbers of departures were observed during the high- and low-lekking seasons (10.6 ± 2.2 vs. 12.6 ± 3.4 observations per mo, respectively; Wilcoxon test: $W = 20$, $P = 0.74$). We considered males to be departing in a group when 2 or more individuals flew ≥ 200 m from the lek in a single direction, with < 120 s elapsing between the first and last departures. Males observed departing the lek in this manner were frequently recorded together subsequently away from the lek, either via opportunistic observation of color-banded individuals or in the context of previously published radio telemetry work (Karubian et al. 2012). Instances of singly departing males were also recorded and used in analyses. In a small number of departures (~10%), females were observed leaving the lek

Table 2. Forms of off-lek sociality reported for lek-mating birds in the published literature. Both within and between species, our literature review demonstrates considerable variability in the form and degree of off-lek sociality in lekking birds. The context in which sociality was observed (e.g., during foraging, during non-breeding season, etc.) is denoted in superscript. Types of sociality are defined as follows: solitary (individual occurring alone); pairs (two birds of opposite or unspecified sex); all-male groups (two or more males); all-female groups (two or more females); mixed-sex groups (groups of three or more containing both adult males and females); juvenile male groups (two or more juvenile males); and unspecified conspecific groups (groups of three or more for which age or sex composition was not reported). *Lek type*: classical = males display in visual and auditory contact of one another; cooperative = males perform joint or coordinated displays within the same territory; exploded = males display within auditory but not visual contact of one another; solitary = male display territories are not clustered in auditory contact of one another. *Variability rating*: the total number of different off-lek sociality types reported for a given species.

Family	Species	Lek type	Types of off-lek sociality reported							Variability rating	References
			Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups		
Cotingidae	*Cephalopterus glabricollis*	Exploded							X[§]	1	Kirwan and Green, 2011
	Cephalopterus ornatus	Exploded	X[*]	X[*]					X[*]	3	Kirwan and Green, 2011
	Cephalopterus penduliger	Exploded	X[*,f]	X[*]	X[*,f]	X[*,f]	X[*,f]			5	Berg, 2000; Tori et al. 2008; Karubian et al. 2010; Scofield et al. 2012; this study
	Lipaugus ater	Cooperative	X[g]							1	Kirwan and Green, 2011
	Lipaugus fuscocinereus	Classical	X[f,g]	X[f]						2	Kirwan and Green, 2011; Trail, 1990
	Lipaugus unirufus	Unreported	X[g]							1	Billerman et al. 2020
	Lipaugus uropygialis	Unreported	X[*]	X[*]						2	Kirwan and Green, 2011
	Lipaugus vociferans	Exploded or classical	X[*,f]						X[*,f]	2	Cohn-Haft et al. 1997; Kirwan and Green, 2011; Jullien and Thiollay 1998; Trail, 1990
	Perissocephalus tricolor	Classical	X[*]		X[*]	X[*]		X[*]		4	Snow, 1972; Trail, 1990
	Phoenicircus carnifex	Exploded	X[g]				X[*]			2	Cohn-Haft et al. 1997; Jullien and Thiollay 1998; Trail and Donahue, 1991
	Procnias albus	Unreported	X[g]			X[f]				2	Bleiweiss, 1997; Kirwan and Green, 2011; Snow, 1982
	Procnias averano	Exploded	X[g]			X[f]				2	Billerman et al. 2020; Bleiweiss, 1997; Kirwan and Green, 2011
	Procnias nudicollis	Unreported				X[f]		X[f]		2	Bleiweiss, 1997; Kirwan and Green, 2011; Snow, 1982
	Procnias tricarunculatus	Exploded	X[g]		X[§]			X[f,g]	X[§,g]	4	Billerman et al. 2020; Kirwan and Green, 2011; Snow, 1977
	Pyroderus scutatus	Classical	X[g]							1	Kirwan and Green, 2011; Trail, 1990
	Rupicola peruvianus	Classical	X[*]		X[*]					2	Kirwan and Green, 2011
	Rupicola rupicola	Classical	X[f]							1	Kirwan and Green, 2011; Jullien and Thiollay 1998

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported							Variability rating	References
			Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups		
Otididae	*Ardeotis australis*	Exploded	X[g]	X[g]	X[*,§]	X[§]			X[f,g]	5	Billerman et al. 2020; Ziembicki, 2010
	Ardeotis kori	Exploded or solitary	X[§,g]	X[g]					X[g]	3	Billerman et al. 2020; Lichtenberg and Hallager, 2008
	Ardeotis nigriceps	Exploded							X[§]	1	Billerman et al. 2020; Morales et al. 2001
	Chlamydotis undulata	Exploded or solitary	X[d]	X[c]	X[f]		X[§,f]			4	Hingrat et al. 2007; Lesobre et al. 2010; Morales et al. 2001
	Eupodotis afra	Exploded	X[g]				X[f]			2	Billerman et al. 2020; Morales et al. 2001
	Lissotis melanogaster	Exploded	X[f]	X[f]						2	Billerman et al. 2020; Morales et al. 2001
	Neotis denhami	Exploded							X[f]	1	Billerman et al. 2020; Morales et al. 2001
	Neotis ludwigii	Exploded							X[f]	1	Billerman et al. 2020; Morales et al. 2001
	Otis tarda	Exploded	X[g]		X[§]	X[§]	X[§]	X[g]		5	Bretagnolle et al. 2022; Morales et al. 2000; Morales and Martín, 2002; Palacín et al. 2011
	Tetrax tetrax	Exploded	X[g]				X[§]		X[§]	3	Bretagnolle et al. 2022; García de la Morena et al. 2015; Villers et al. 2010
Oxyruncidae	*Oxyruncus cristatus*	Exploded	X[f]	X[f]						2	Billerman, 2020; Kirwan and Green, 2011
Paradisaeidae	*Astrapia mayeri*	Unreported	X[f]	X[f]		X[f]				3	Billerman et al. 2020; Bleiweiss, 1997
	Astrapia stephaniae	Classical	X[f]	X[f]					X[f]	3	Billerman et al. 2020
	Paradisaea apoda	Classical	X[*]			X[g]				2	Billerman et al. 2020
	Paradisaea guilielmi	Classical	X[f]		X[f]					2	Billerman et al. 2020

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported: Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups	Variability rating	References
Paradisaeidae (cont.)	*Parotia carolae*	Exploded					X[f]			1	Billerman et al. 2020
	Parotia lawesii	Exploded or solitary	X[d]	X[c]						2	Beehler and Pruett-Jones, 1983; Pruett-Jones and Pruett-Jones, 1990; Billerman et al. 2020
	Pteridophora alberti	Exploded	X[f]							1	Billerman et al. 2020; Beehler and Pruett-Jones, 1983
	Semioptera wallacii	Classical							X[f]	1	Billerman et al. 2020; Beehler and Pruett Jones, 1983
Phasianidae	*Argusianus argus*	Exploded	X[g]							1	Winarni, 2002
	Centrocercus minimus	Classical	X[g]		X[§]	X[§]	X[*]			4	Billerman et al. 2020
	Centrocercus urophasianus	Classical	X[§]		X[§]	X[*,§]	X[*]	X[*,§]		5	Bailey, 1925; Beck, 1977; Dunn and Braun, 1986; Gibson and Bradbury, 1987; Scott, 1942
	Lyrurus tetrix	Classical or solitary			X[*,§]	X[§]	X[*,§]			3	Angelstam, 1984; Billerman et al. 2020; Kruijt et al. 1972; Drovetski et al. 2006; Robel, 1969; Wiley, 1991
	Meleagris gallopavo	Classical, harem, or lek-like	X[§]		X[*]	X[*,§]	X[*]	X[§]		5	Billerman et al. 2020; Krakauer, 2008; Watts and Stokes, 1971
	Pavo cristatus	Exploded, classical, or harem	X[g]		X[§]	X[§]	X[g]			4	Billerman et al. 2020; Petrie et al. 1991; Yasmin, 1997
	Tetrao urogalloides	Classical			X[§]	X[§]	X[§]			3	Andreev, 1991; Billerman et al. 2020; Drovetski et al. 2006
	Tetrao urogallus	Classical	X[§]		X[§]	X[§]				3	Billerman et al. 2020
	Tympanuchus cupido	Classical	X[§]	X[§]	X[*,§]	X[*,§]	X[§]			5	Billerman et al. 2020; Lehmann, 1941; Sharpe, 1968
	Tympanuchus pallidicinctus	Classical	X[g]		X[*]	X[§]			X[g]	4	Billerman et al. 2020; Sharpe, 1968
	Tympanuchus phasianellus	Classical or solitary	X[d]	X[*]	X[*,§]	X[§]			X[g]	5	Billerman et al. 2020; Lumsden, 1965; Sexton, 1979

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported							Variability rating	References
			Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups		
Pipridae	*Ceratopipra chloromeros*	Exploded						X[*]		1	Tello, 2001
	Ceratopipra erythrocephala	Classical	X[*]		X[*]		X[*]	X[*]		4	Billerman et al. 2020; Cohn-Haft et al. 1997; Lill, 1976; Snow, 1962b; Théry, 1992; Jullien and Thiollay 1998
	Ceratopipra mentalis	Exploded	X[*]							1	Billerman et al. 2020; Kirwan and Green, 2011
	Chiroxiphia boliviana	Cooperative	X[*]							1	Billerman et al. 2020
	Chiroxiphia lanceolata	Cooperative							X[f]	1	Friedmann and Smith, 1950
	Chiroxiphia linearis	Cooperative	X[*]		X[*]			X[*]		3	Billerman et al. 2020; Foster et al. 1977
	Corapipo altera	Exploded			X[*,f,†]		X[f]			2	Jones et al. 2014
	Corapipo gutturalis	Exploded or mobile	X[f]	X[f]	X[f]					3	Kirwan and Green, 2011; Prum, 1986; Jullien and Thiollay 1998
	Corapipo leucorrhoa	Exploded	X[*]	X[*]			X[*]			3	Kirwan and Green, 2011; Stiles and Skutch, 1989
	Heterocercus aurantiivertex	Exploded or solitary	X[g]	X[g]						2	Kirwan and Green, 2011
	Ilicura militaris	Exploded	X[f]	X[f]		X[f]			X[f]	4	Kirwan and Green, 2011
	Lepidothrix iris	Exploded or solitary	X[g]	X[g]						2	Billerman et al. 2020; Kirwan and Green, 2011
	Lepidothrix serena	Classical or exploded	X[f]	X[f]			X[*]			3	Prum, 1985; Théry 1990; Théry, 1992; Jullien and Thiollay 1998

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported: Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups	Variability rating	References
Pipridae (cont.)	*Manacus aurantiacus*	Exploded	X[*]							1	Kirwan and Green, 2011; Stiles and Skutch, 1989
	Manacus manacus	Classical	X*[d]		X[*]	X[*]	X[*]	X[*]		5	Hilty 2003; Kirwan and Green, 2011; Lill, 1974b; Théry, 1992
	Manacus vitellinus	Classical	X[*]							1	Wetmore, 1972
	Masius chrysopterus	Exploded	X[f]	X[f]					X[f]	3	Kirwan and Green, 2011; Prum and Johnson, 1987
	Neopelma chrysocephalum	Exploded	X[g]							1	Kirwan and Green, 2011
	Neopelma pallescens	Exploded							X[f]	1	Kirwan and Green, 2011
	Pipra fasciicauda	Exploded	X[*]							1	Kirwan and Green, 2011
	Pipra filicauda	Exploded			X[*]					1	Ryder et al. 2006
	Pseudopipra pipra	Exploded or solitary	X[*]				X[*]			2	Kirwan and Green, 2011; Théry, 1992; Jullien and Thiollay 1998
	Tyranneutes stolzmanni	Exploded or solitary	X[g]							1	Foster, 2021; Kirwan and Green, 2011
	Tyranneutes virescens	Exploded	X[f]							1	Kirwan and Green, 2011; Jullien and Thiollay 1998
	Xenopipo atronitens	Exploded	X[g]						X[f]	2	Kirwan and Green, 2011; Prum, 1990
Ploceidae	*Euplectes jacksoni*	Exploded							X[§]	1	Billerman et al. 2020; van Someren, 1958; Wambugu and Nzilani, 2008
Pycnonotidae	*Eurillas latirostris*	Classical	X[g]						X[f]	2	Billerman et al. 2020; Trail, 1990
Scolopacidae	*Calidris pugnax*	Classical	X[d]	X[c]	X[*]	X[*]	X[*]			5	Bachman and Widemo, 1999; Lank and Smith, 1987, 1992; van Rhijn, 1983; Wiley, 1991
	Calidris subruficollis	Classical or solitary	X[d]	X[c]					X[§]	3	Billerman et al. 2020; Lanctot et al. 1997; Pruett-Jones, 1988; Trail, 1990
	Gallinago hardwickii	Classical	X[g]						X[g]	2	Billerman et al. 2020; Iida, 1995
	Gallinago media	Classical	X[f]						X[f]	2	Billerman et al. 2020; Trail, 1990

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported							Variability rating	References
			Solitary	Pairs	All-male groups	All-female groups†	Mixed-sex groups†	Juvenile male groups	Unspecified conspecific groups		
Tityridae	*Laniocera rufescens*	Exploded	X[f]							1	Billerman et al. 2020; Kirwan and Green, 2011; Robinson et al. 2000
	Laniocera hypopyrra	Exploded	X[f]							1	Billerman et al. 2020; Cohn-Haft et al. 1997; Kirwan and Green, 2011
Trochilidae	*Amazilia tzacatl*	Unreported	X[g]			X[n]				2	Billerman et al. 2020
	Amazilia rutila	Exploded or solitary	X[g]							1	Billerman et al. 2020
	Campylopterus hemileucurus	Unreported	X[g]							1	Billerman et al. 2020
	Chlorestes candida	Unreported	X[g]							1	Billerman et al. 2020
	Eutoxeres aquila	Exploded	X[g]							1	Billerman et al. 2020; Stiles and Skutch, 1989; Trail, 1990
	Phaethornis bourcieri	Unreported	X[g]							1	Cohn-Haft et al. 1997; Jullien and Thiollay 1998
	Phaethornis guy	Unreported	X[*]	X[*]						2	Billerman et al. 2020; Snow, 1974
	Phaethornis longuemareus	Classical	X[f]							1	Jullien and Thiollay 1998; Trail, 1990
	Phaethornis ruber	Unreported	X[f]							1	Jullien and Thiollay 1998
	Pampa rufa	Exploded	X[g]							1	Billerman et al. 2020; Trail, 1990
	Phaethornis superciliosus	Classical	X[*]							1	Cohn-Haft et al. 1997; Stiles and Wolf, 1979; Jullien and Thiollay 1998; Trail, 1990
	Polyerata amabilis	Exploded	X[f]							1	Billerman et al. 2020
	Polyerata decora	Unreported	X[f]							1	Billerman et al. 2020
	Topaza pella	Unreported	X[f,g]							1	Cohn-Haft et al. 1997; Jullien and Thiollay 1998
Tyrannidae	*Mionectes oleagineus*	Classical, exploded, or solitary	X[d,g]	X[c]						2	Billerman et al. 2020; Westcott and Smith 1994

Table 2. Continued

Family	Species	Lek type	Types of off-lek sociality reported: Solitary	Pairs	All-male groups	All-female groups[†]	Mixed-sex groups[†]	Juvenile male groups	Unspecified conspecific groups	Variability rating	References
Viduidae	*Vidua chalybeata*	Exploded or solitary							X[§]	1	Billerman et al. 2020; Payne and Payne, 1977; Payne, 1984
	Vidua macroura	Exploded	X[f]						X[§]	2	Billerman et al. 2020; Shaw, 1984
	Vidua obtusa	Unreported	X[f]	X[f]			X[f]		X[§]	4	Billerman et al. 2020
	Vidua orientalis	Unreported	X[f]						X[f]	2	Billerman et al. 2020
	Vidua paradisaea	Exploded					X[§]		X[*f]	2	Billerman et al. 2020; Payne and Payne, 1977
Percent of represented species exhibiting sociality type			83	26	25	23	23	10	29		

[†]May include juveniles.
[*]Observations away from the lek site.
[§]Observations during non-breeding and/or migratory periods.
[c]Off-lek copulations known to occur, so off-lek pair inferred.
[d]Some males display solitarily away from leks as an alternative mating strategy.
[f]Foraging observation.
[g]General occurrence description.
[n]Females may nest colonially.

alongside males; however, because such instances were fairly rare, only the number of males departing the lek was considered in our analyses. Data presented here are mainly from three well-studied focal leks (leks 1, 3, and 4; Ottewell et al. 2018). We also included $n = 5$ observations from 2 other leks (leks 7 and 8), as adding or dropping these observations did not influence qualitative results. We did not typically monitor leks after the morning bout of activity and initial male departure; therefore, we were unable to analyze the size and timing of groups returning to the lek.

Between 2002 and 2018, we recorded the behavior and group size of any umbrellabirds observed away from leks, defined as > 100 m from the nearest lek. Observations occurred opportunistically as trained observers gathered data for other projects in and around the 3,500-ha BBS property, which encompasses 5 known umbrellabird leks. More specifically, umbrellabirds were one of the small number of "priority species" for which researchers gathered location, sociality, foraging, and behavioral data every time they were encountered. Upon detecting a bird or group, we documented the number of other individuals observed within 20 m during a 60 s period. Both lone individuals and groups were recorded and used in analyses. The vast majority of observations were single-sex (i.e., all-male or all-female) groups. Mixed-sex groups were also observed, but these were uncommon (<9% of all observations; Supplementary Material Table S1) and thus excluded from the comparisons of all-male and all-female groups. We included no more than one all-male and one all-female observation per day in our analyses to ensure that the same individuals were not counted multiple times in a given day; if more than one single-sex group was observed in a day, we used the larger group for analysis. We choose the larger group, rather than a random group, for the following reasons: (1) choice of observation did not influence qualitative results; (2) the rule was applied consistently for all seasons and for all group types, and thus does not bias group size estimates toward a particular sex or season; and (3) choosing the larger group captured the behavior of a greater number of individuals in the population on a given day. Effort was constant across the annual cycle, and similar numbers of off-lek sociality observations occurred during high- and low-lekking months (44.4 ± 3.0 vs. 35.0 ± 5.7 observations, respectively; Wilcoxon test: $W = 7$, $P = 0.11$).

Foraging observations occurred opportunistically between 2002 and 2018 as part of the protocol researchers followed during priority-species encounters in the field (see above). If off-lek foraging was observed, we recorded the resource (i.e., fruit, insect, or vertebrate) that the individual or group was exploiting. Consumption of a resource at a given location and time was considered as a single event, regardless of the quantity consumed or the number of individuals involved. In rare instances ($n = 2$), umbrellabirds consumed both fruits and insects during the same foraging observation; these were excluded from analysis. The total number of fruit and animal foraging observations per month were summed across years to characterize the diet of males and females throughout the annual cycle. Although observation effort was similar across both seasons, there was a non-significant tendency for more foraging observations during the high-lekking season than the low-lekking season (16.9 ± 2.7 vs. 8.8 ± 3.9 observations per month, respectively; Wilcoxon test: $W = 6$, $P = 0.07$).

Statistical analyses.

All analyses were conducted in R (version 4.2.2; R Core Team 2021). We fit two models to determine whether the size and coordination of male groups departing the lek differed between the high- and low-lekking seasons (August–February and March–July, respectively). First, we compared group sizes between the two seasons by fitting a generalized linear mixed-effects model (GLMM) with a Poisson error distribution using the *LME4* package in *R* (Bates et al. 2015). This model included male departing group size as the response variable, season (i.e., high- vs. low-lekking) as the predictor variable, and lek ID as a random effect. In the cases where multiple departures were observed in the same morning, we used the largest group size for analysis (see justification above). Because an increase in the departing group size during the high-lekking season could simply be the result of an increase in lek attendance, we also calculated a "coordination index" by dividing the departing group size by the total number of males present at the lek. This metric accounts for seasonal variation in lek attendance. We then fit a Bayesian zero-one-inflated beta regression model using the *BRMS* package in *R* (Bürkner 2017) to determine whether departure coordination varied by season. This class of mixture model accommodates a response variable with a continuous-discrete distribution—in this case, a continuously varying proportion with a probability mass at 1—by incorporating both beta and degenerate distributions (Ospina and Ferrari 2012). Our model included the coordination index as the response variable, season as the predictor variable, and lek ID and year as random effects. If multiple group departures were recorded on a given day, we calculated a coordination index for each departure and averaged the coordination indices. For this analysis, we excluded instances where the departing individual was the only individual present at the lek, as these departures would be scored as perfectly coordinated despite only involving one individual. To test for the existence of an effect, we used the package *BAYESTESTR* to obtain the probability of direction (pd), which was then used to calculate the Bayesian equivalent of the frequentist *P*-value (Makowski et al. 2019a, 2019b). The *z*-score of the model output was estimated by taking the quotient of the effect-size estimate and the standard error. We also report Bayesian estimates of effect significance, which are obtained by comparing the degree of overlap between a region of practical equivalence (ROPE) and the collected data (Kruschke 2014). Model assumptions were checked using the *R* package *DHARMA* (Hartig 2018).

To determine whether the size of male and female off-lek groups varied throughout the year, we fit a GLMM with a zero-truncated negative binomial distribution (quadratic parameterization) using the *R* package *GLMMTMB* (Brooks et al. 2017). The model included the following: foraging group size as the response variable; season, sex, and their interaction as predictor variables; year as a random effect; and an autoregressive error structure to account for temporal autocorrelation between months. Because many individuals in the study population were not color-banded, it was not always possible to link off-lek individuals to a particular lek; thus, we did not include a random effect of lek in this model. We used the *DHARMA* package (Hartig 2018) to confirm that the model met assumptions. We also tested specific between-group comparisons using non-parametric Wilcoxon rank-sum tests.

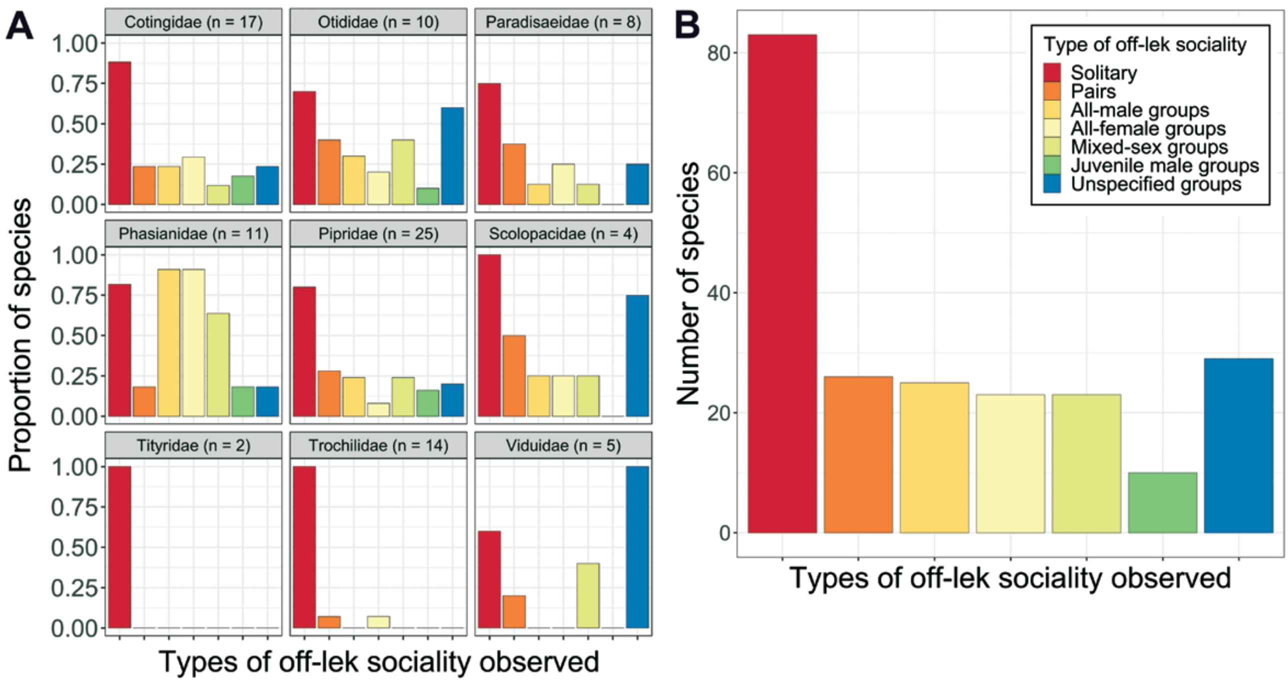

Figure 1. Diversity of off-lek sociality in lek-mating birds. (A) Frequency of different forms of off-lek sociality in families of lekking birds for which data were available. Only families with >1 species with available off-lek sociality data are shown. Proportions were calculated as the number of species in the family reported to exhibit a given off-lek sociality type divided by the total number of species in the family for which off-lek sociality data were available. (B) Total number of lekking species reported to exhibit each type of off-lek sociality, independent of family. Note that individual species may exhibit multiple forms of off-lek sociality and thus may be represented more than once in each graphic. The legend in panel (**B**) applies to both panels.

Finally, we fit generalized least squares (GLS) regression models in *NLME* (Pinheiro et al. 2017) to determine whether monthly patterns of lekking activity and/or fruit foraging predicted levels of off-lek sociality for either sex. All response and predictor variables in the models were monthly averages across all years of the study. For males, the multiple regression model included average male off-lek group sizes as the response variable and average number of males at the lek (a proxy for lekking activity) and proportion of fruit in the male diet as predictor variables. An autoregressive error structure was incorporated into the model to account for temporal autocorrelation between months. The same model was used for females, except that proportion of fruit in the female diet was the only predictor variable. To determine the monthly proportion of fruit in the diet for each sex, we divided the number of fruit foraging observations in a given month by the total number of foraging observations for a given month (Supplementary Material Figure S1). All descriptive statistics are presented as means ± 1 SEM unless otherwise stated.

RESULTS

Literature Review

Our review of the published literature provided information about off-lek sociality for 100 species of lek-mating birds across 13 avian families (Table 2). Available information about off-lek social interactions in lekking birds is largely limited to anecdotal reports, suggesting that our current understanding is likely incomplete. Nonetheless, this review demonstrates considerable diversity in the form and degree of off-lek sociality, both within and between species and families of birds (Figure 1A).

Across all species and families, solitary behavior away from the lek was most common (83% of all species), followed by pairs (26%), all-male groups (25%), all-female groups (23%), mixed-sex groups (23%), and juvenile male groups (10%) (Figure 1B). Another 29% of species were reported to occur in conspecific groups of unspecified composition. Several avian families were highly diverse in their off-lek social behavior, with at least some species engaging all types of off-lek sociality (e.g., Cotingidae, Otididae, Phasianidae, and Pipridae; Figure 1A). Additionally, certain families were disproportionately likely to exhibit particular forms of off-lek sociality: for instance, nearly all Phasianidae species for which data was available form sex-segregated (i.e., all-male or all-female) flocks, especially during the winter, while all Trochilidae reportedly occur solitarily away from the lek (Figure 1A).

Within manakins (Pipridae), the family for which we had the most data ($n = 25$ species across 13 genera), we visualized the diversity of off-lek sociality types alongside the recently published phylogeny for the group (Leite et al. 2021). Manakin species exhibit diverse types of off-lek social behavior, reportedly occurring in pairs (7 species), all-male groups (6 species), mixed-sex groups (6 species), juvenile male groups (4 species), all-female groups (2 species), and/or solitarily (20 species) (Figure 2). Broadly, off-lek sociality in the family appears to be a relatively labile trait, with numerous gains and losses of sociality types among closely related species. It is also noteworthy that most members of the subfamily Neopelminae (3 of 4 species; 75%) were reported to only occur solitarily away from the lek, whereas most members of the subfamily Piprinae (16 of 21 species; 76%)—generally characterized by more elaborate male characters and lekking behavior—were reported to exhibit some

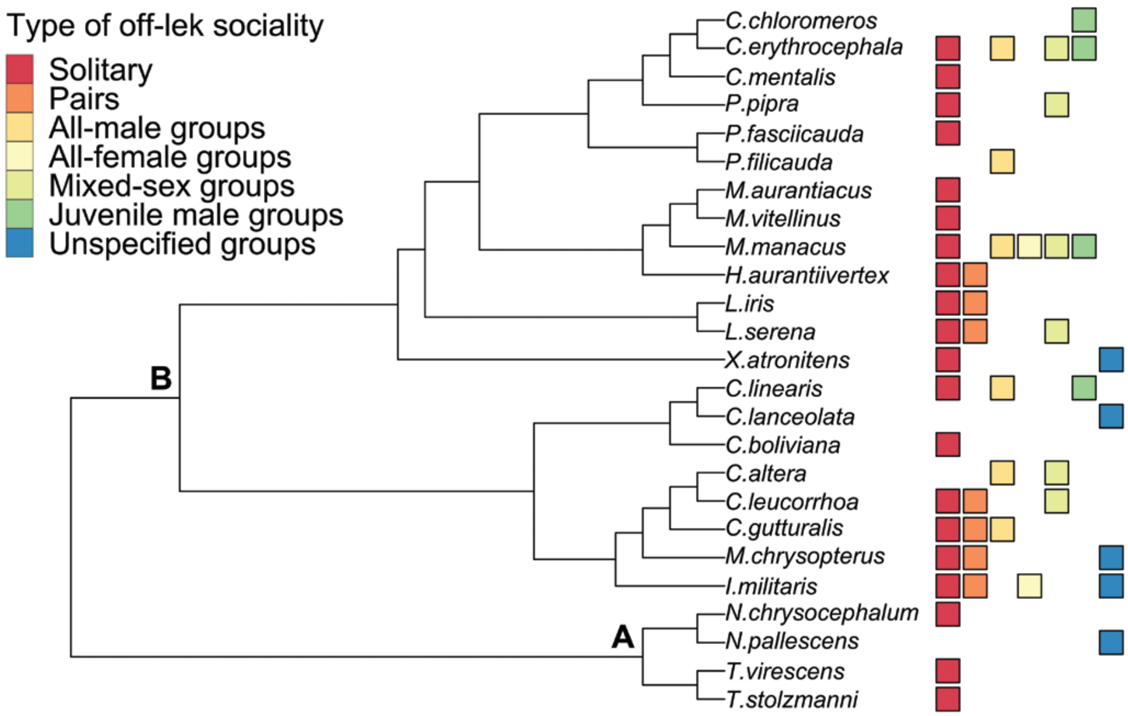

Figure 2. Phylogenetic representation of off-lek sociality in Pipridae. Available off-lek sociality information (colored rectangles) is shown alongside the manakin phylogeny, which comprises the subfamilies Neopelminae (A) and Piprinae (B). Manakin species for which no off-lek sociality information was available (n = 25) and/or lekking behavior has not been reported (n = 4) were omitted from the tree.

form of off-lek sociality. We emphasize that few studies to date have been specifically focused on documenting off-lek social behavior, and thus the diversity of off-lek sociality types in Pipridae is likely to be underrepresented. While the details of this phylogenetic visualization would almost certainly change with more targeted study, it does exemplify the 2 take-home points of our literature review: (1) information is incomplete or missing for many lekking species, even among the best-studied groups; and (2) there is clearly substantial variation in the form and degree of off-lek sociality, both within and among species.

Case Study in Umbrellabirds

Aggregation at fruit resources does not drive off-lek sociality.

We next focus on a more detailed evaluation of competing hypotheses for the adaptive significance of off-lek sociality in Long-wattled Umbrellabirds (see Table 1). We recorded 161 off-lek foraging events during the study period, which were used to assess the incidental aggregation and resource acquisition hypotheses. A similar number of foraging observations were recorded for female (n = 86) and male (n = 72) birds, and very few mixed-sex groups were observed actively foraging (n = 3). Umbrellabirds were observed consuming fruits (n = 106), insects (n = 53), and frogs (n = 2). Fruits composed a relatively higher proportion of the male diet year-round, while females showed a more definitive shift toward frugivory during the high-lekking season (Supplementary Material Figure S1); this is perhaps due to greater reliance by females on insects during nesting periods, which primarily occur in the low-lekking season during the rainier parts of the year (Tori et al. 2008). We observed no significant difference in the size of groups that were actively consuming fruit compared to those that were not, with actively foraging groups tending to be smaller than groups that were not actively foraging (1.5 ± 0.11 vs. 1.62 ± 0.07, respectively; Wilcoxon test: W = 20788, P = 0.19). This result suggests that incidental aggregation at shared fruit resources is not a primary factor shaping off-lek group formation in umbrellabirds.

Male departing groups are larger and more coordinated during the high-lekking season.

We monitored the size and coordination of male umbrellabird departures from the lek site, hypothesizing that male departing groups would be larger and more coordinated during the high-lekking season (per the reproductive benefits hypothesis). We observed 151 total instances of male umbrellabirds departing the lek, 80.1% of which occurred in groups of two or more individuals. The number of males observed departing the lek together averaged 3.49 individuals (± 0.15; range: 1–10). Male departing group sizes were significantly larger during the high-lekking season than the low-lekking season (4.51 ± 0.19 vs. 2.51 ± 0.21; GLMM: z = 5.70, P < 0.0001; Figure 3A). Furthermore, male departing groups were significantly more coordinated during the high-lekking season compared to the low-lekking season (coordination index: 0.89 ± 0.02 vs. 0.70 ± 0.04; BRM: z = –2.58; P = 0.01; Figure 3B). In Bayesian terms, the effect of the low-lekking season on departure coordination had a 99.42% probability of being negative relative to the high-lekking season (median = –0.63; 95% CI: –1.10, –0.16) and can be considered significant (1.12% in full ROPE; Makowski et al. 2019b). These results are consistent with key predictions of the reproductive benefits hypothesis and fail to support the incidental

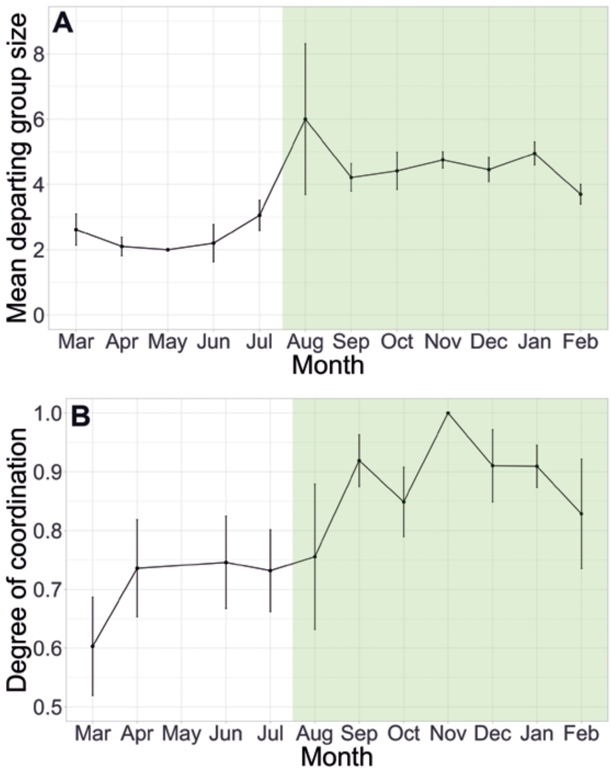

Figure 3. Size and coordination of male umbrellabird groups departing the lek. (A) Average size of male groups departing the lek varied throughout the year. Departing groups were significantly larger during the high-lekking season (August through February; shaded in green) than the low-lekking season (March through July; unshaded). (B) Male departing groups were significantly more coordinated during the high-lekking season (shaded in green) than the low-lekking season. Degree of coordination is calculated as the proportion of males departing together divided by the total number of males present at the lek. Error bars represent ± 1 SEM.

aggregation hypothesis (Table 1). However, the resource acquisition hypothesis also predicts coordinated departures from the lek site (Table 1), and periods of high lekking activity overlap with periods of high frugivory (Supplementary Material Figure S1). Thus, further analysis was required to distinguish between these two hypotheses (see below).

Males exhibit greater off-lek sociality during the high-lekking season.

The reproductive benefits hypothesis predicts that male off-lek groups during the high-lekking season should be larger than female groups during the high-lekking season and larger than male groups during the low-lekking season. During the study period, we collected 486 independent observations of umbrellabirds away from the lek (Supplementary Material Table S1). All-male groups were significantly larger than all-female groups (1.72 ± 0.11 vs. 1.24 ± 0.04; GLM: $z = 5.36$, $P < 0.0001$). Although the main effect of seasonality was not significant in predicting off-lek group sizes ($z = 0.85$, $P` = 0.39$), there was a significant interaction effect between sex and seasonality ($z = 3.53$, $P = 0.0004$), reflecting the increase in male group sizes (1.90 ± 0.14 vs. 1.24 ± 0.14; Wilcoxon test: $W = 2990.5$, $P = 0.002$) but not female group sizes (1.19 ± 0.03 vs. 1.30 ± 0.07; Wilcoxon test: $W = 8326.5$, $P = 0.22$) during the high-lekking season (Figure 4).

Lek attendance but not foraging behavior predicts off-lek sociality.

If reproductive benefits are the primary factor driving male off-lek group formation in umbrellabirds, male lek attendance (i.e., average number of males at the lek each month) should predict off-lek male group sizes. Alternatively, if off-lek sociality is primarily driven by foraging benefits, then the degree to which individuals are relying on fruit resources—estimated by proportion of fruit in the diet—should predict off-lek group sizes for each sex. In a multiple regression, lek attendance significantly predicted off-lek male group sizes (GLS: $t = 3.22$, df = 8, $P = 0.01$; Pearson's correlation: $r = 0.58$), while monthly proportion of fruit in the diet did not (GLS: $t = 0.75$, df = 8, $P = 0.47$; Pearson's correlation: $r = 0.30$). Dietary fruit proportion also failed to predict off-lek group sizes for females (GLS: $t = -1.46$, df = 10, $P = 0.17$; Pearson's correlation: $r = -0.28$).

DISCUSSION

Diversity in Off-Lek Sociality in Lekking Birds

Our literature review revealed considerable diversity in off-lek sociality among lek-mating birds. While the factors driving this variation remain largely unexplored, it seems likely that some combination of predation pressure, foraging ecology, reproductive incentives, and resource availability influence the observed patterns. In general, we expect predation to be a major force driving the flocking behavior observed in many Phasianidae and Scolopacidae species, which often occupy open habitats and may face considerable predator pressure (Page and Whitacre 1975, Angelstam 1984). On the other hand, foraging ecology is likely to be particularly important for shaping patterns of sociality in frugivores (e.g., cotingas, manakins, birds-of-paradise), which may increase fruit-finding success or efficiency by foraging in groups, and trap-lining nectarivores (e.g., hermit hummingbirds), which must take distinct and solitary routes to maximize individual nectar payoffs from flowers (Gill 1988). Of course, predation and foraging are not mutually exclusive and may interact in complex ways with one another (Beauchamp 2022) and other variables (e.g., lek structure, habitat, mating skew) to produce diverse off-lek behavioral strategies, even among closely related species. For instance, species in the manakin family, which likely face similar predation pressure and exhibit "redundant" foraging ecologies (Loiselle et al. 2007), apparently vary widely in the types of off-lek sociality they exhibit.

Many important questions remain about the ways in which off-lek sociality may be linked to processes of sexual selection in lek-mating organisms. Do all-male associations away from the lek (observed in cotingas: Snow 1982, Tori et al. 2008, Trail 1990; grouse: Robel 1969; and manakins: Snow 1962b, Lill 1974b, Foster 1977, Ryder et al. 2006) allow males to coordinate lek attendance and mitigate the reproductive costs of leaving the lek to forage? Analogously, does off-lek cohesion among females facilitate synchronized lek visitation (reported in bustards: Bretagnolle et al. 2022; cotingas: Trail 1985; grouse: Lehmann 1941; and manakins: Théry 1992), which may in turn influence associated sexual selection processes such as mate-choice copying and copulation disruption? In what ways might off-lek juvenile practice groups (observed in grouse: Dunn and Braun 1986; and manakins: Snow 1962a,

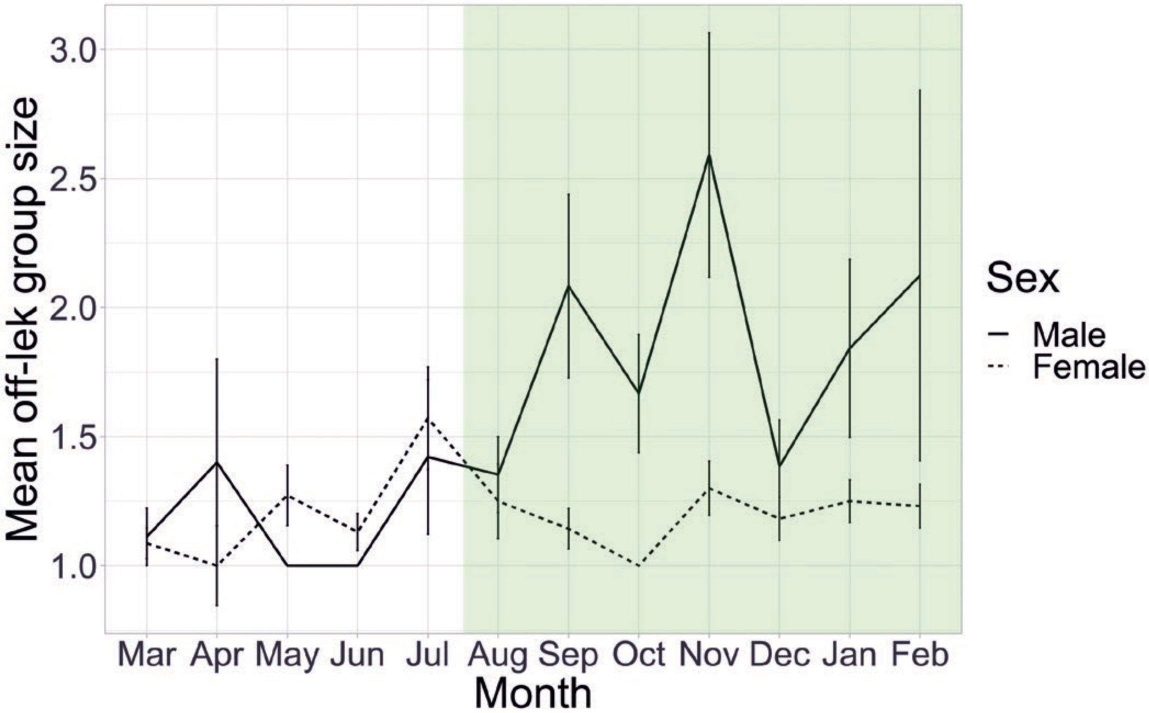

Figure 4. Comparison of male and female off-lek group sizes during the high- and low-lekking seasons. Off-lek male groups were significantly larger during the high-lekking season (shaded in green) compared to the low-lekking season (unshaded). Female off-lek group sizes did not differ between seasons. In addition, male groups were significantly larger than female groups during the high-lekking but not the low-lekking season. Error bars represent ± 1 SEM.

1962b, Tello 2001) or off-lek interactions with adult males (reported in cotingas: Snow 1977; and manakins: Jones et al. 2014) shape the ontogeny of complex display repertoires? To what extent do interactions in sex-segregated or mixed-sex winter flocks influence social networks, dominance hierarchies, and mating outcomes during the subsequent breeding season (Rintamaki et al. 1999, Sharpe 1968)?

As illustrated by this subset of unanswered questions, our review points to the need for further research into the adaptive significance of off-lek social behavior. Little is known about the form or function of these behaviors for the vast majority of lekking species, and published data are coarse and largely anecdotal in nature. More detailed examinations of off-lek sociality patterns—particularly in species that exhibit sex-based, seasonal, or age-specific differences in sociality—are likely to advance our understanding of the behavioral and sexual selection dynamics in lekking species.

Case Study in Umbrellabirds

To our knowledge, this work on umbrellabirds constitutes the first detailed assessment of off-lek sociality patterns in a lekking bird across sexes and seasons. Our data support the hypothesis that off-lek sociality in umbrellabirds is primarily driven by male-specific reproductive incentives related to lek mating. During the high-lekking season, males exhibited a marked shift toward increased off-lek sociality in the form of larger and more coordinated group departures from the lek and larger cohesive groups away from the lek. In contrast, female off-lek sociality was generally low and did not increase during the high-lekking season, suggesting that the selective pressures driving off-lek group formation primarily apply to breeding males. Alternatively, females may be disincentivized from behaving socially during nesting periods: solitary foraging may be less likely to attract predators to nests, and—given that females primarily provision nests with insects (Karubian et al. 2003, Greeney et al. 2012)—social foraging may yield limited benefits. We did not find support for the hypotheses that off-lek sociality is driven by resource acquisition benefits (the proportion of fruit in the diet failed to predict off-lek group sizes for either sex) or incidental aggregation (males departed the lek in a coordinated manner, and umbrellabirds did not occur in larger groups while actively consuming shared resources). Although we lacked the necessary data to directly test the antipredator hypothesis, we deem it unlikely given that predation attempts on adult umbrellabirds were never recorded in 20 yr of observation by our team and have never been reported elsewhere (Snow 1982). In addition, females (presumably more susceptible to predation due to their ~1.5 times smaller size; Tori et al. 2008) were less likely to occur in off-lek social groups than males. In line with the general support for the reproductive benefits hypothesis, we identify three ways in which off-lek sociality may influence male reproductive success at the lek.

First, off-lek sociality may confer reproductive benefits to males by enabling the synchronization of foraging and display periods. During the study period, male umbrellabirds were frequently observed circling the canopy above the lek prior to departing in one or more groups at the end of early-morning display periods, foraging in groups away from the lek in the middle of the day, and returning to the lek in groups of similar size in the late afternoon (Tori et al. 2008, Karubian and Durães 2014). Female visitation is highest in the early morning and late afternoon, although visits can occur sporadically throughout the day (Karubian and Durães 2014). Coordinating off-lek movements should be particularly important for males that travel considerable distances from their lek sites to forage, as is the case in umbrellabirds (Karubian et al. 2010), as it would otherwise be difficult for males to know when others are returning to the lek. Such coordination may allow males to monitor the display activities of rivals, minimize the amount of time spent displaying while other males are away, and mitigate the reproductive costs of foraging (Rathore et al. 2023). Indeed, greater concurrent lek attendance should yield reproductive benefits to the majority of males by increasing per-capita female visitation rates (Bradbury 1981, Lank and Smith 1992) and reducing male mating skew (Alatalo et al. 1992, Höglund et al. 1993, Widemo and Owens 1995, Hernandez et al. 1999). However, because optimal group size at the lek for a given male is predicted to be dependent upon that individual's relative quality (Widemo and Owens 1995, Hernandez et al. 1999), the propensity to coordinate lek attendance via off-lek sociality may be rank-dependent. If optimal lek size for a given male is negatively related to his quality and high-ranking males stand to benefit the least from achieving large lek sizes (per Widemo and Owens 1995), they may be expected to employ distinct off-lek behavioral strategies (e.g., reduced sociality) relative to low-ranking males. Alternatively, if low-ranking males benefit from shadowing the movements of successful males to and from the lek, the mechanisms driving off-lek group formation may mirror the "hotshot" model of lek evolution (i.e., low-quality males cluster around high-quality ones; Beehler and Foster 1983).

Second, although our results do not support resource acquisition as the primary driver of off-lek sociality in umbrellabirds, increased foraging efficiency may nevertheless be an important subsidiary benefit of off-lek group formation. Males of many lekking species face a direct tradeoff between time spent foraging away from the lek and time spent displaying at the lek (e.g., Lank and Smith 1987), the latter of which is a strong predictor of male mating success (Fiske et al. 1998). If greater off-lek sociality is associated with greater foraging efficiency, socially foraging males should gain increased reproductive opportunities by minimizing time spent away from the lek. Social foraging can also reduce variance in individual foraging success (Thompson et al. 1974, Pulliam and Millikan 1982, Beauchamp 2005), which may be especially important for lekking males due to the high energetic requirements of displaying (Caraco 1981, Vehrencamp et al. 1989, Barske et al. 2014, Cestari et al. 2018). As such, individuals that choose to remain at the lek when others leave to forage could incur reproductive costs on three potential fronts: reduced likelihood of copulation due to smaller group sizes at the lek, reduced time at the lek due to lower solitary foraging efficiency, and reduced energy budget for costly displays due to lower solitary foraging success. This could lead to the evolution of a "local decision rule" wherein individuals depart the lek when their neighbors depart, leading to emergent coordination (Rathore et al. 2023). However, it is notable that group foraging does not always increase the efficiency with which non-renewing resources are exploited (e.g., Beauchamp 2005), and thus the degree to which a given species benefits from social foraging may be context-dependent or driven primarily by the reproductive benefits of such coordination.

Third, males may gain reproductive benefits via interactions with females away from the lek. While the majority of off-lek observations in this study were of either solitary individuals or single-sex groups, some off-lek groups contained individuals of both sexes ($n = 42$). In mixed-sex groups away from the lek, it is possible that females assess potential mates or even copulate, as has been documented in a number of other lekking birds (Lill 1974a, Sexton 1979, Gibson and Bradbury 1987, Lank and Smith 1987, Théry 1992, Lanctot et al. 1997). In line with this possibility, mixed-sex umbrellabird groups were larger and over four times as common during the high-lekking season compared to the low-lekking season (Supplementary Material Table S1).

Additional work is needed to better understand the importance of off-lek sociality in umbrellabirds. A limitation of the current study is that most of our observations were conducted on unmarked males, which reduces our ability to relate individual off-lek behavioral strategies to fitness outcomes. For example, we were unable to confirm whether individuals at leks that exhibit cohesive off-lek social groups experience higher per-capita mating success, a key prediction of the reproductive benefits hypothesis that remains to be tested. Whether males experience ontogeny in levels of sociality as they rise in the lek hierarchy, and whether "floater" males differ from territorial males in their tendency for off-lek sociality, also remain open questions. More broadly, we suggest that a better understanding of individual incentives within leks and the role of group coordination in shaping reproductive outcomes may provide insight into the mechanisms driving and maintaining lek formation in a variety of taxa. Evolutionary game theory (Maynard Smith 1984) may provide a useful analytical framework for exploring how individual incentives, and optimal off-lek behavioral strategies, vary among males at a given lek in relation to the behaviors of lek-mates.

Quantifying off-lek sociality can be logistically challenging, and future studies may benefit from integrating opportunistic and standardized approaches to off-lek behavioral surveying. For example, we combined a systematic methodology for surveying lek departures (which occurred predictably at the end of morning activity bouts) with off-lek observations that were primarily opportunistic. Automated proximity loggers—which register the frequency and duration of contact between tagged individuals (Drewe et al. 2012)—would facilitate better understanding of the strength and coordination off-lek associations. Traditional radio telemetry, particularly when multiple individuals from a given lek are tracked simultaneously, may also yield important insights into the form and degree of off-lek associations (e.g., Robel 1969). With or without tracking technology, systematic observations of fruit trees and other resources near lek sites may also prove useful in assessing the degree of sociality and cohesion during off-lek forays (e.g., Lill 1974b). Lastly, population monitoring that spans both breeding and nonbreeding periods—and ideally incorporates measures of resource availability (e.g., Boyle 2010)—is likely to be especially fruitful in illuminating the correlates of male and female sociality across the full annual cycle.

Conclusions

This study is intended to provide a conceptual framework for understanding the off-lek component of lekking species' behavioral ecology. We consider it likely that off-lek sociality influences, and is influenced by, sexual selection dynamics in these systems. For instance, the observed patterns in umbrellabirds are consistent with the hypothesis that reproductive incentives for group cohesion drive increased male off-lek sociality during the breeding season. More broadly, the degree to which males benefit from coordinating lek attendance may depend upon multiple interacting factors, including the degree of mating skew at the lek, the dispersion and predictability of food resources across the landscape, male home range size and lek structure, the predictability of daily activity patterns at the lek, and predator pressure away from the lek. In addition, non-mating factors (e.g., resource acquisition, predator avoidance, and incidental aggregation) may play larger roles in shaping off-lek behavioral strategies in systems where basic biology and life history factors differ from umbrellabirds. The considerable diversity in both the form and degree of off-lek sociality provides a rich, but currently underexplored, lens through which to deepen our understanding of the behavioral ecology of lek-breeding organisms.

Supplementary Material

Supplementary material is available at *Ornithology* online.

Acknowledgments

We are grateful for the support of FCAT (Fundación para la Conservación de los Andes Tropicales), the Jatun Sacha Foundation, and the Ecuadorian Ministry of the Environment. We thank D. Cabrera, F. Castillo, M. Reardon, D. Mosquera, and many others for assistance in the field; T. Ramirez-Parada for contributions to preliminary data analysis; and members of the Karubian lab for valuable feedback. R. Ribeiro, A. Gunderson, and anonymous reviewers provided helpful comments on the manuscript.

Funding statement

This work was supported by the Conservation, Food & Health Foundation; Disney Worldwide Conservation Fund; the National Science Foundation (EAGER 1548548 to J.K. and a Graduate Research Fellowship to H.L.A.); the National Geographic Society; Tulane University; the Tinker Foundation and the Stone Center for Latin American Studies; and the United States Fish & Wildlife Service (NMBCA 6318 to J.K.).

Ethics statement

All research was conducted with approval of the Ecuadorian Ministry of the Environment (MAE–DNB–CM–2015–0017) and the Tulane University IACUC (Protocol ID: 1550).

Conflict of interest statement

The authors declare no conflicts of interest.

Author contribution

H.L.A. conducted the literature review, analyzed the data, and wrote the original manuscript; J.O. and J.K. collected data; H.L.A. and J.K. revised the manuscript. All authors have approved the final version of the manuscript.

Data availability

Analyses reported in this article can be reproduced using the data provided by Anderson et al. (2023).

LITERATURE CITED

Alatalo, R. V., J. Höglund, and W. J. Sutherland (1992). Evolution of Black Grouse leks: Female preferences benefit males in larger leks. *Behavioral Ecology* 3:53–59.

Anderson, H. L., J. Olivo, and J. Karubian (2023). Data from: The adaptive significance of off-lek sociality in birds: A synthetic review, with evidence for the reproductive benefits hypothesis in Long-wattled Umbrellabirds. *Ornithology* 140:ukad021. https://doi.org/10.5061/dryad.xsj3tx9m5.

Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ, USA.

Andreev, A. V. (1991). Winter habitat segregation in the sexually dimorphic Black-billed Capercaillie *Tetrao urogalloides*. *Ornis Scandinavica* 22:287–291.

Angelstam, P. (1984). Sexual and seasonal differences in mortality of the Black Grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica* 15:123–134.

Bachman, G., and F. Widemo (1999). Relationships between body composition, body size, and alternative reproductive tactics in a lekking sandpiper, the Ruff (*Philomachus pugnax*). *Functional Ecology* 13:411–416.

Bailey, A. M. (1925). Segregation of the sexes in the sage-hen. *The Condor* 27:172–173.

Barske, J., L. Fusani, M. Wikelski, N. Y. Feng, M. Santos, and B. A. Schlinger (2014). Energetics of the acrobatic courtship display in male Golden-collared Manakins (*Manacus vitellinus*). *Proceedings of the Royal Society B: Biological Sciences* 281:20132482.

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

Beauchamp, G. (2005). Does group foraging promote efficient exploitation of resources? *Oikos* 111:403–407.

Beauchamp, G. (2022). Flocking in birds is associated with diet, foraging substrate, timing of activity, and life history. *Behavioral Ecology and Sociobiology* 76:74.

Beck, T. D. I. (1977). Sage grouse flock characteristics and habitat selection in winter. *The Journal of Wildlife Management* 41:18–26.

Beehler, B. M., and M. S. Foster (1983). Hotshots, hotspots, and female preference in the organization of lek mating systems. *The American Naturalist* 131:203–209.

Beehler, B., and S. G. Pruett-Jones (1983). Display dispersion and diet of birds of paradise: A comparison of nine species. *Behavioral Ecology and Sociobiology* 13:229–238.

Berg, K. S. (2000). Field notes on the biology of the Long-wattled Umbrellabird *Cephalopterus penduliger* in west Ecuador. *Cotinga* 14:26–29.

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg (Editors) (2020). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY. https://www.birdsoftheworld.org/bow/home.

BirdLife International (2020). Species factsheet: *Cephalopterus penduliger*.

Bleiweiss, R. (1997). Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds. *Evolutionary Ecology* 11:217–235.

Boyle, W. A. (2010). Does food abundance explain altitudinal migration in a tropical frugivorous bird? *Canadian Journal of Zoology* 88:204–213.

Bradbury, J. W. (1981). The evolution of leks. In *Natural Selection and Social Behavior* (R. D. Alexander and D. Tinkle, Editors). Chiron Press, New York, NY, USA. pp. 13–169.

Bretagnolle, V., J. Traba, and M. B. Morales (2022). *Little Bustard: Ecology and Conservation*. Wildlife Research Monographs, Vol. 5, Springer Nature, Switzerland.

Brooks, M. E., K. Kasper, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, and B. Bolker (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400.

Bürkner, P.-C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* 80:1–28.

Buskirk, W. H. (1976). Social systems in a tropical forest avifauna. *The American Naturalist* 110:293–310.

Caraco, T. (1981). Risk-sensitivity and foraging groups. *Ecology* 62:527–531.

Cestari, C., B. A. Loiselle, and M. A. Pizo (2016). Trade-offs in male display activity with lek size. *PloS One* 11:e0162943.

Cestari, C., M. A. Pizo, and B. A. Loiselle (2018). Display activity and foraging costs of a frugivorous lekking bird. *The Wilson Journal of Ornithology* 130:869–873.

Clark, C. W., and M. Mangel (1984). Foraging and flocking strategies: Information in an uncertain environment. *The American Naturalist*, 123:626–641.

Cohn-Haft, M., A. Whittaker, and P. C. Stouffer (1997). A new look at the "species-poor" central Amazon: The avifauna north of Manaus, Brazil. In *Studies in Neotropical ornithology Honoring Ted Parker* (J. V. Remsen, Jr., Editor). *Ornithological Monographs* 48:205–235.

Drewe, J. A., N. Weber, S. P. Carter, S. Bearhop, X. A. Harrison, S. R. X. Dall, R. A. McDonald, and R. J. Delahay (2012). Performance of proximity loggers in recording intra- and inter-specific interactions: A laboratory and field-based validation study. *PLoS One* 7:e39068.

Drovetski, S. V., S. Rohwer, and N. A. Mode (2006). Role of sexual and natural selection in evolution of body size and shape: A phylogenetic study of morphological radiation in grouse. *Journal of Evolutionary Biology* 19:1083–1091.

Dunn, P. O., and C. E. Braun (1986). Late summer-spring movements of juvenile sage grouse. *The Wilson Bulletin* 98:83–92.

DuVal, E. H., and B. Kempenaers (2008). Sexual selection in a lekking bird: The relative opportunity for selection by female choice and male competition. *Proceedings of the Royal Society B: Biological Sciences* 275:1995–2003.

Egert-Berg, K., E. R. Hurme, S. Grief, A. Goldstein, L. Harten, L. G. M. Herrera, J. J. Flores-Martínez, A. T. Valdes, D. S. Johnston, O. Eitan, I. Borissov, J. R. Shipley, R. A. Medellin, G. S. Wilkinson, H. R. Goerlitz, and Y. Yovel (2018). Resource ephemerality drives social foraging in bats. *Current Biology* 28:3667–3673.

Fiske, P., P. T. Rintamäkki, and E. Karvonen (1998). Mating success in lekking males: A meta-analysis. *Behavioral Ecology* 9:328–338.

Foster, M. S. (1977). Odd couples in manakins: A study of social organization and cooperative breeding in *Chiroxiphia linearis*. *The American Naturalist* 111:845–853.

Foster, M. S. (2021). Male aggregation in Dwarf-tyrant Manakins and what it tells us about origins of leks. *Integrative and Comparative Biology* 61:1310–1318.

Foster, W. A., and J. E. Treherne (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293:466–467.

Friedmann, H., and F. D. Smith, Jr. (1950). A contribution to the ornithology of northeastern Venezuela. *Proceedings of the United States National Museum* 100:501.

García de la Morena, E. L., M. B. Morales, G. Bota, J. P. Silva, A. Ponjoan, F. Suárez, S. Mañosa, and E. de Juana (2015). Migration patterns of Iberian Little Bustards *Tetrax tetrax*. *Ardeola* 62:95–112.

Gibson, R. M., and J. W. Bradbury (1987). Lek organization in sage grouse: Variations on a territorial theme. *The Auk* 104:77–84.

Gill, F. B. (1988). Trapline foraging by Hermit Hummingbirds: Competition for an undefended, renewable resource. *Ecology* 69:1933–1942.

Greeney, H. F., G. M. Kirwan, and E. T. Miller (2012). Nesting biology of the Long-wattled Umbrellabird *Cephalopterus penduliger*. Part II: Nestling provisioning. *Cotinga* 34:23–27.

Hartig, F. (2018). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package, v. 0.2.0. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Hernandez, M. L., A. I. Houston, and J. M. McNamara (1999). Male rank and optimal lek size. *Behavioral Ecology* 10:73–79.

Hilty, S. L. (2003). Birds of Venezuela. Princeton University Press, Princeton, NJ, USA.

Hingrat, Y., M. Saint Jaime, F. Ysnel, E. L. Nuz, and F. Lacroix (2007). Habitat use and mating system of the Houbara Bustard (*Chlamydotis undulata undulata*) in a semi-desertic area of North Africa: Implications for conservation. *Ibis* 148:39–52.

Höglund, J., and R. V. Alatalo (1995). *Leks*. Princeton University Press, Princeton, NJ, USA.

Höglund, J., R. Montgomerie, and F. Widemo (1993). Costs and consequences of variation in the size of Ruff leks. *Behavioral Ecology and Sociobiology* 32:31–39.

Iida, T. (1995). Ecological significance of daily periodicity in display flight of the Latham's Snipe *Gallinago hardwickii*: A study on the presence of lek breeding system. *Japanese Journal of Ornithology* 44:219–227.

Ioannou C. C., F. Bartumeus, J. Krause, and G. D. Ruxton (2011). Unified effects of aggregation reveal larger prey groups take longer to find. *Proceedings of the Royal Society B: Biological Sciences* 278:2985–2990.

Jones, M. A., E. H. DuVal, and W. A. Boyle (2014). Individual and temporal variability in the courtship behavior of White-ruffed Manakins (*Corapipo altera*), a species with facultative cooperative displays. *The Auk* 131:727–742.

Jullien, M., and J.-M. Thiollay (1998). Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. *Journal of Animal Ecology* 67:227–252.

Karubian, J., G. Castañeda, J. F. Freile, R. T. Salazar, T. Santander, and T. B. Smith (2003). Breeding biology and nesting behavior of the Long-wattled Umbrellabird *Cephalopterus penduliger* in northwestern Ecuador. *Bird Conservation International* 13:351–360.

Karubian, J., and R. Durães (2014). Impacts of mating behavior on plant-animal seed dispersal mutualisms: A case study from a Neotropical lek-breeding bird. In *Sexual Selection: Perspectives and Models from the Neotropics* (R. H. Macedo and G. Machado, Editors). Elsevier, London, UK. pp. 365–390.

Karubian, J., R. Durães, J. L. Storey, and T. B. Smith (2012). Mating behavior drives seed dispersal by the Long-wattled Umbrellabird *Cephalopterus penduliger*. *Biotropica* 44:689–698.

Karubian, J., V. L. Sork, T. Roorda, R. Durães, and T. B. Smith (2010). Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology* 19:1745–1753.

Kirkpatrick, M., and M. J. Ryan (1991). The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38.

Kirwan, G. M., and G. Green (2011). *Cotingas and Manakins*. Princeton University Press, Princeton, NJ, USA.

Kokko, H., P. T. Rintamäki, R. V. Alatalo, J. Höglund, E. Karvonen, and A. Lundberg (1999). Female choice selects for lifetime lekking performance in Black Grouse males. *Proceedings of the Royal Society B* 266:2109–2115.

Krakauer, A. H. (2008). Sexual selection and the genetic mating system of wild turkeys. *The Condor* 110:1–12.

Krebs, J. R., M. H. MacRoberts, and J. M. Cullen (1972). Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* 114:507–530.

Kruijt, J. P., G. J. de Vos, and I. Bossema (1972). The arena system of Black Grouse, *Lyrurus tetrix tetrix* (L.). *Proceedings of the International Ornithological Congress* 15:399–423.

Kruschke, J. K. (2014). Rejecting or accepting parameter values in Bayesian estimation. *Advances in Methods and Practices in Psychological Science* 1:270–280.

Lanctot, R. B., K. T. Scribner, B. Kempenaers, and P. J. Weatherhead (1997). Lekking without a paradox in the Buff-breasted Sandpiper. *The American Naturalist* 149:1051–1070.

Landeau, L., and J. Terborgh (1986). Oddity and the "confusion effect" in predation. *Animal Behaviour* 34:1372–1380.

Lank, D. B., and C. M. Smith (1987). Conditional lekking in Ruff (*Philomachus pugnax*). *Behavioral Ecology and Sociobiology* 20:137–145.

Lank, D. B., and C. M. Smith (1992). Females prefer larger leks: Field experiments with Ruffs (*Philomachus pugnax*). *Behavioral Ecology and Sociobiology* 30:323–329.

Lehmann, V. W. (1941). Attwater's prairie chicken its life history and management. *North American Fauna* 57:1–65.

Leite, R. N., R. T. Kimball, E. L. Braun, E. P. Derryberry, P. A. Hosner, G. E. Derryberry, M. Anciães, J. S. McKay, A. Aleixo, C. C. Ribas, R. T. Brumfield and J. Cracraft (2021). Phylogenomics of manakins (Aves: Pipridae) using alternative locus filtering strategies based on informativeness. *Molecular Phylogenetics and Evolution* 155:107013.

Lesobre, L., F. Lacroix, E. L. Nuz, Y. Hingrat, T. Chalah, and M. Saint Jaime (2010). Absence of male reproductive skew, along with high frequency of polyandry and conspecific brood parasitism in the lekking Houbara Bustard *Chlamydotis undulata undulata*. *Journal of Avian Biology* 41:117–127.

Lichtenberg, L. M., and S. Hallager (2008). A description of commonly observed behaviors for the Kori Bustard (*Ardeotis kori*). *Journal of Ethology* 26:17–34.

Lill, A. (1974a). Sexual behavior of the lek-forming White-bearded Manakin (*Manacus manacus trinitatis* Hartert). *Zeitschrift für Tierpsychologie* 36:1–36.

Lill, A. (1974b). Social organization and space utilization in the lek-forming White-bearded Manakin, *M. manacus trinitatus* Hartert. *Zeitschrift für Tierpscyhologie* 36:513–530.

Lill, A. (1976). Lek behavior in the golden-headed manakin, *Pipra erythrocephala* in Trinidad (West Indies). *Fortschritte der Verhaltensforschung* 18:83.

Loiselle, B. A., P. G. Blendinger, J. G. Blake, and T. B. Ryder (2007). Ecological redundancy in seed dispersal systems: A comparison between manakins (Aves: Pipridae) in two tropical forests. In *Seed Dispersal: Theory and Its Application in a Changing World* (A. J. Dennis, Editor). CAB International, Wallingford, UK. pp. 178–195.

Lumsden, H. G. (1965). *Displays of the sharp-tailed grouse*. Ontario Department of Lands and Forests, Maple, Ontario, Canada.

Mackenzie, A., J. D. Reynolds, V. J. Brown, and W. J. Sutherland (1995). Variation in male mating success on leks. *The American Naturalist* 145:633–652.

Makowski, D., M. S. Ben-Schachar, S. H. A. Chen, and D. Lüdecke (2019a). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology* 10:2767.

Makowski, D., M. S. Ben-Schachar, and D. Lüdecke (2019b). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software* 4:1541.

Maynard Smith, J. (1984). Game theory and the evolution of behaviour. *Behavioral and Brain Sciences* 7:95–101.

McDonald, D. B., and W. K. Potts (1994). Cooperative display and relatedness among males in a lek-mating bird. *Science* 266:1030–1032.

Morales, M. B., J. C. Alonso, J. A. Alonso, and E. Martin (2000). Migration patterns in male Great Bustards (*Otis tarda*). *The Auk* 117:493–498.

Morales, M. B., F. Jiguet, and B. Arroyo (2001). Exploded leks: What bustards can teach us. *Ardeola* 48:85–98.

Morales, M. B., and C. A. Martín (2002). *Otis tarda* Great Bustard. *BWP Update* 4:217–232.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. de Fonseca, and J. Kent (2000). Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.

Ospina, R., and S. L. P. Ferrari (2012). A general class of zero-or-one-inflated beta regression models. *Computational Statistics and Data Analysis* 56:1609–1623.

Ottewell, K., L. Browne, D. Cabrera, J. Olivo, and J. Karubian (2018). Genetic diversity of dispersed seeds is highly variable among leks of the Long-wattled Umbrellabird. *Acta Oecologica* 86:31–37.

Page, G., and D. F. Whitacre (1975). Raptor predation on wintering shorebirds. *The Condor* 77:73–83.

Palacín, C., J. C. Alonso, J. A. Alonso, M. Magaña, and C. A. Martín (2011). Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the Great Bustard *Otis tarda*. *Journal of Avian Biology* 42:301–308.

Paradis, E., J. Claude, and K. Strimmer (2004). APE: Analyses of phylogenetics and evolution in the R language. *Bioinformatics* 20:289–290.

Payne, R. B. (1984). *Sexual Selection, Lek and Arena Behavior, and Sexual Size Dimorphism in Birds*. Ornithological Monographs, #33, American Ornithologists' Union, Washington, D.C., USA.

Payne, R. B., and K. Payne (1977). Social organization and mating success in local song populations of village indigobirds, *Vidua chalybeata*. *Zeitschrift für Tierpsychologie* 45:113–173.

Petrie, M., T. Halliday, and C. Sanders (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour* 41:323–331.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, J. Ranke, and R Core Team (2017). Package "nlme." Linear and nonlinear mixed-effects models, v. 3.1. https://cran.r-project.org/package=nlme

Pruett-Jones, S. G. (1988). Lekking versus solitary display: temporal variations in dispersion in the buff-breasted sandpiper. *Animal Behaviour* 36:1740–1752.

Pruett-Jones, S. G. and M. A. Pruett-Jones (1990). Sexual selection through female choice in Lawes' parotia, a lek-mating bird of paradise. *Evolution* 44:486–501.

Prum, R. O. (1985). Observations of the White-fronted Manakin (*Pipra serena*) in Suriname. *The Auk* 102:384–387.

Prum, R. O. (1986). The displays of the White-throated Manakin *Corapipo gutturalis* in Suriname. *Ibis* 128:91–102.

Prum, R. O. (1990). Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). *Ethology* 84:202–231.

Prum, R. O., and A. E. Johnson (1987). Display behavior, foraging ecology, and systematics of the Golden-winged Manakin (*Masius chrysopterus*). *The Wilson Bulletin* 99:521–784.

Pulliam, H. R., and G. C. Millikan (1982). Social organization in the nonreproductive season. In *Avian Biology*, *Vol.* VI (D. S. Farner, J. R. King, and K. C. Parkes, Editors), Academic Press, New York, NY, USA. pp. 169–197.

Rathore, A., K. Isvaran, and V. Guttal (2023). Lekking as collective behaviour. *Philosophical Transactions of the Royal Society B* 378:20220066.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rintämaki, P. T., E. Karvonen, R. V. Alatalo, and A. Lundberg (1999). Why do males perform on lek sites outside the breeding season? *Journal of Avian Biology* 30:359–366.

Robel, R. J. (1969). Movements and flock stratification within a population of blackcocks in Scotland. *Journal of Animal Ecology* 38:755–763.

Robinson, W. D., J. D. Brawn, and S. K. Robinson (2000). Forest bird community structure in Central Panama: Influence of spatial scale and biogeography. *Ecological Monographs* 70:209–235.

Rowe, L., and D. Houle (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society B: Biological Sciences* 263:1415–1421.

Ryder, T. B., J. G. Blake, and B. A. Loiselle (2006). A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. *The Auk* 123:247–258.

Scofield, D. G., P. E. Smouse, J. Karubian, and V. L. Sork (2012). Use of alpha, beta, and gamma diversity measures to characterize seed dispersal by animals. *The American Naturalist* 180:719–732.

Scott, J. W. (1942). Mating behavior of the sage grouse. *The Auk* 59:477–498.

Sexton, D. A. (1979). Off-lek copulation in Sharp-tailed Grouse. *The Wilson Bulletin* 91:150–151.

Sharpe, R. S. (1968). *The evolutionary relationships and comparative behavior of prairie chickens. Doctoral dissertation*, The University of Nebraska-Lincoln, Lincoln, NB, USA.

Shaw, P. (1984). The social behavior of the Pin-tailed Whydah *Vidua macroura* in northern Ghana. *Ibis* 126:463–473.

Shogren, E. H., and W. A. Boyle (2021). Spread the word: Male manakins advertise the presence of display sites with neighboring competitors. *Animal Behaviour* 177:147–158.

Shorey, L., S. Piertney, J. Stone, and J. Höglund (2000). Fine-scale genetic structuring on *Manacus manacus* leks. *Nature* 408:352–353.

Snow, D. W. (1962a). A field study of the black and white manakin, *Manacus manacus*, in Trinidad. *WI Zoologica* 47:67–104.

Snow, D. W. (1962b). A field study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, W. I. *WI Zoologica* 47:183–198.

Snow, B. K. (1972). A field study of the calfbird *Perissocephalus tricolor*. *Ibis* 114:139–162.

Snow, B. K. (1974). Lek behaviour and breeding of Guy's hermit hummingbird *Phaethornis guy. Ibis* 116:278–297.

Snow, B. K. (1977). Territorial behavior and courtship of the male Three-wattled Bellbird. *The Auk* 94:623–645.

Snow, D. W. (1982). *The Cotingas: Bellbirds, Umbrellabirds, and Other Species*. Cornell University Press, Ithaca, NY, USA.

Stiles, F. G., and A. F. Skutch (1989). *Guide to the Birds of Costa Rica*. Cornell University Press, Ithaca, NY, USA.

Stiles, F. G., and L. L. Wolf (1979). *Ecology and Evolution of Lek Mating Behavior in the Long-tailed Hermit Hummingbird*. Ornithological Monographs, no. 27, American Ornithologists' Union, Washington, D.C., USA.

Tello, J. G. (2001). Lekking behavior of the Round-tailed Manakin. *The Condor* 103:298–321.

Théry, M. (1990). Display repertoire and social organization of the white-fronted and white-throated manakins. *The Wilson Bulletin* 102:123–130.

Théry, M. (1992). The evolution of leks through female choice: Differential clustering and space utilization in six sympatric manakins. *Behavioral Ecology and Sociobiology* 30:227–237.

Thompson, W. A., I. Vertinsky, and J. R. Krebs (1974). The survival value of flocking in birds. *Journal of Animal Ecology* 43:785–820.

Tinbergen, N. (1951). *The Study of Instinct*. Oxford University Press, Oxford, UK.

Tori, W. P., R. Durães, T. B. Ryder, M. Anciães, J. Karubian, R. H. Macedo, J. A. C. Uy, P. G. Parker, T. B. Smith, A. C. Stein, M. S. Webster, J. G. Blake, and B. A. Loiselle (2008). Advances in sexual selection theory: insights from Neotropical avifauna. *Ornitologia Neotropical* 19:151–163.

Trail, P. W. (1985). A lek's icon: The courtship display of a Guianan cock-of-the-rock. *American Birds* 39:235–240.

Trail, P. W. (1990). Why should lek-breeders be monomorphic? *Evolution* 44:1837–1852.

Trail, P. W., and P. Donahue (1991). Notes on the behavior and ecology of the red-cotingas (Cotingidae: *Phoenicircus*). *The Wilson Bulletin* 103:539–768.

van Rhijn, J.G. (1983). On the maintenance and origin of alternative strategies in the Ruff *Philomachus pugnax*. *Ibis* 125:482–498.

van Someren, V. D. (1958). *A Bird Watcher in Kenya*. Oliver and Boyd, London, UK.

Vehrencamp, S. L., J. W. Bradbury, and R. M. Gibson (1989). The energetic cost of display in male sage grouse. *Animal Behaviour* 38:885–896.

Villers, A., A. Millon, F. Jiguet, J.-M. Lett, C. Attie, M. B. Morales, and V. Bretagnolle (2010). Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: Releasing birds from Spain threatens attempts to conserve declining French populations. *Ibis* 152: 254–261.

Wambugu, G. M., and J. Nzilani (2008). Population status of Jackson's Widowbird *Euplectes jacksoni* in Mau Narok-Molo grasslands Important Bird Area, Kenya. *Scopus* 27:10–18.

Ward, P., and A. Zahavi (1973). The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* 115:517–534.

Watts, C. R., and A. W. Stokes (1971). The social order of turkeys. *Scientific American* 224:112–119.

Westcott, D. A., and J. N. M. Smith (1994). Behavior and social organization during the breeding season in *Mionectes oleagineus*, a lekking flycatcher. *The Condor* 96:672–683.

Wetmore, A. (1972). *The Birds of Panama, Part 3*. Smithsonian Press, Washington, D.C., USA.

Widemo, F., and I. P. F. Owens (1995). Lek size, male mating skew and the evolution of lekking. *Nature* 373:148–151.

Wiley, R. H. (1991). Lekking in birds and mammals: Behavioral and evolutionary issues. *Advances in the Study of Behavior* 20:201–291.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, MA, USA.

Winarni, N. L. (2002). *The abundance and distribution patterns of Great Argus Pheasant (Argusianus argus) in Bukit Barisan Selatan National Park, Sumatra, Indonesia. Master's thesis*, The University of Georgia, Athens, GA, USA.

Yasmin, S. (1997). Group size and composition of Indian peafowl (*Pavo cristatus*) in an agro-ecosystem at Aligarh, Uttar Pradesh. *The Journal of the Bombay Natural History Society* 94:478–482.

Ziembicki, M. (2010). *Ecology and movements of the Australian Bustard Ardeotis australis in a dynamic landscape. Doctoral dissertation*, University of Adelaide, Adelaide, SA, Australia.