

CHARACTERISTICS AND SEXUAL FUNCTIONS OF SKY-DANCING DISPLAYS IN A SEMI-COLONIAL RAPTOR, THE MONTAGU'S HARRIER (*CIRCUS PYGARGUS*)

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ABSTRACT.—Raptors perform spectacular aerial displays, but our understanding of their complexity and functions is still limited. We describe the characteristics of Montagu's Harrier (*Circus pygargus*) sky-dancing displays and evaluate possible sexual functions. Sky-dancing was performed by both sexes, but much more frequently by males. Although occurring throughout the breeding season and into the post-fledging period, sky-dancing displays by males were more frequent during the pre-laying period (from 3 wk before laying, when pair formation is occurring, until just after laying onset). Pre-laying display frequency by males and females increased with colony size and vole abundance. A principle component analysis on display characteristics (height, speed, number of loops, twists, undulations, and calls) identified three main axes (PC1-3). PC1 correlated with all parameters, identifying displays that started at higher altitude, descended at higher speeds, with higher frequencies of twists, undulations, loops, and displaying calls. PC2 opposed high and fast displays with low complexity (in terms of twist and undulation frequency) to displays that were slower, started from lower altitude, but were more complex. PC3 contrasted displays with loops to others with undulations. PC1 scores differed between sexes, with males having more intense displays (greater PC1 scores) than females. Male displays were more intense in larger colonies and when voles were more abundant, but less intense when wind speed increased, or when males displayed while carrying prey. Variation in PC2 and PC3 scores in males was mostly explained by wind conditions: displays started higher and were faster when there was no wind, and aerial displays tended to have more loops instead of undulations in more windy conditions. Our results support the hypothesis that Montagu's Harrier sky-dancing displays performed during the pre-laying period, particularly the most elaborate ones, are costly to produce and may thus potentially honestly advertise individual quality. Additionally, our observations were consistent with the hypothesis that these displays have both intra- and intersexual functions.

KEY WORDS: *Montagu's Harrier; Circus pygargus; competition; courtship behavior; display; flying agility; handicap principle; sexual selection.*

CARACTERÍSTICAS Y FUNCIONES SEXUALES DE LOS DESPLIEGUES DEL BAILE AÉREO EN *CIRCUS PYGARGUS*, UNA RAPAZ SEMI-COLONIAL

RESUMEN.—Las rapaces ejecutan espectaculares despliegues aéreos, pero nuestro entendimiento de su complejidad y funciones es todavía limitado. Describimos las características de los despliegues del baile aéreo y evaluamos sus posibles funciones sexuales. El baile aéreo fue realizado por ambos sexos, pero con mayor frecuencia por los machos. Aunque ocurren durante toda la estación reproductiva y en el periodo pos-volantón, los despliegues del baile aéreo por parte del macho fueron más frecuentes durante el periodo pre-puesta de huevos (desde tres semanas anteriores a la puesta, cuando la formación de parejas

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ocurre, hasta justo después de la puesta). La frecuencia del despliegue pre-puesta de machos y hembras aumentó con el tamaño de la colonia y la abundancia de topillos. Un análisis de componentes principales de las características del despliegue (altura, velocidad, número de vueltas, giros, ondulaciones y llamados) identificó tres ejes principales (CP1-3). El CP1 se correlacionó con todos los parámetros, identificando despliegues que comenzaron a una mayor altitud, descendieron a velocidades mayores, con mayor frecuencia de giros, ondulaciones, vueltas y llamados de despliegue. El CP2 enfrentó despliegues altos, veloces y de menor complejidad (en términos de frecuencia de giros y ondulaciones) con despliegues más lentos, que comenzaron a una altitud menor, pero que fueron más complejos. El CP3 contrastó los despliegues con vueltas contra otros despliegues con ondulaciones. Los puntajes del CP1 difirieron entre sexos, con los machos realizando despliegues más intensos (puntajes del CP1 mayores) que las hembras. Los despliegues de los machos resultaron más intensos en las colonias de mayor tamaño y cuando los ratones de campo fueron más abundantes, pero los despliegues fueron menos intensos cuando la velocidad del viento aumentó o cuando los machos realizaron el despliegue portando una presa. La variación en los puntajes del CP2 y CP3 en los machos fue explicada, en mayor parte, por las condiciones del viento: los despliegues comenzaron a mayor altitud y fueron más veloces cuando no hubo viento, y los despliegues aéreos tendieron a tener más vueltas en vez de ondulaciones en condiciones más ventosas. Nuestros resultados apoyan la hipótesis de que los despliegues del baile aéreo de *Circus pygargus* ejecutados durante el periodo pre-puesta, particularmente los más elaborados, son costosos de producir y pueden, por lo tanto, potencialmente ser un indicador honesto de la calidad individual. Adicionalmente, nuestras observaciones fueron consistentes con la hipótesis de que estos despliegues poseen funciones intra- e inter-sexuales.

[Traducción del equipo editorial]

Many raptors perform spectacular aerial displays, which have fascinated raptor biologists for many years. Although there are several descriptive accounts of these displays (Ross 1941, Jepson 1986, Pandolfi and Barocci 1994, Debus 1995), our understanding of their complexity and functions is still relatively limited (Simmons 1991). Aerial displays may have many different functions, including conspecific attraction to certain sites (feeding sites, roosts, or breeding areas, Simmons 1991, Pandolfi and Barocci 1994), social cohesion, pair bonding, and training of young (Pandolfi and Pino d'Astoro 1994, Pandolfi 1996) or predator deterrence (Sternalski and Bretagnolle 2010). Additionally, they may have sexual functions, including mate attraction and mate choice, as well as agonistic functions in a context of intrasexual competition (Simmons 1988, 1991, Mougeot et al. 2001, Wiacek 2004).

In the context of sexual selection, the frequency, complexity, or intensity of aerial displays may honestly advertise individual quality as a potential mate or competitor. For raptors, other signals of individual quality may include the quality of the territory or nest site (Newton 1979, Sergio et al. 2011), plumage or bare-part color intensity (Negro et al. 1998, Bortolotti et al. 2003, Mougeot and Arroyo 2006), or feeding rate (Simmons 1988, Mougeot et al. 2002). The latter is very relevant to raptors, as in many species males provide most of the food to females and offspring during courtship and the nesting season (Newton 1979). However, this type

of signal (food delivery rate) is not immediately visible to the female and takes time to evaluate, which makes it less efficient to evaluate several potential mates simultaneously.

According to the Handicap Principle, an honest signal of individual quality should be costly to produce or maintain (Zahavi 1975), and the relative cost or handicap associated with the display should be greater for lower-quality individuals, such that only high-quality individuals can afford to produce or maintain better signals (Grafen 1990). For aerial displays, this cost might involve complexity, intensity, maneuverability, safety, or the energetic cost of repetition. Producing a more elaborate display may imply greater risk-taking, and may require better physical condition or greater flying ability. Therefore, certain types of display may be affordable only by certain individuals. Another possible handicap may involve performing aerial displays under adverse conditions; for instance, when food is scarce or when wind speed is greater and flight maneuverability impaired. Finally, some raptors occasionally display with prey in their talons. Birds must adjust their flight speed when transporting food, because they are more constrained metabolically and aerodynamically (Hedenstrom and Alerstam 1995). Therefore, carrying food while performing an aerial display might be a handicap, and such a performance may advertise a better-quality individual.

Among raptors, harriers (*Circus spp.*) have different aerial displays, among which "sky-dancing" aerial

displays are best known (Simmons 1988, 1991, Pandolfi and Barocci 1994, Debus 1995, Wiacek 2004). The Montagu's Harrier (*Circus pygargus*) is a socially monogamous bird, but changes partners almost systematically among years (mate fidelity from year to year is <15%, V. Bretagnolle unpubl. data). It is also migratory, and the time for mate assessment is limited to the time between arrival and clutch initiation. This ground-nesting raptor is semicolonial, and may nest either solitarily or in loose aggregations or colonies (see Arroyo 1999, Arroyo et al. 2001). Colonial breeding may facilitate mate choice, allowing the simultaneous assessment of potential mates at colony sites (Wagner 1992, Danchin and Wagner 1997). Aerial displays of Montagu's Harriers likely play a role in mate choice, but our understanding of the characteristics or functions of these aerial displays is still very limited in this species, as well as in other raptors.

In this report, we describe the characteristics of Montagu's Harrier sky-dancing displays in terms of their frequency of occurrence, structure, and complexity, and we evaluate possible sexual functions. We first examined their occurrence (frequency) throughout the breeding season, and in relation to food abundance and colony size. A function in pairing and mate choice predicts a higher frequency of displays upon arrival (early in the pre-laying period) when new pairs are forming. Males are the main providers of food, and mate choice should be mostly in terms of a female choice of a male. Therefore, aerial displays should be performed by males much more than females. An agonistic function of aerial displays predicts that displays also should be frequent when females are fertile (and when male-male competition for fertilizations is greatest; Mougeot et al. 2001, 2006). Intra- and intersexual competition both increase with density, so aerial display frequency also should increase with colony size. Second, we examined differences in the structure and complexity of aerial displays. We predicted male displays would be more elaborate than female displays. We also evaluated the potential costs of performing more complex displays, as predicted by the Handicap Principle (Zahavi 1975). We predicted displays would be less elaborate in less favorable environmental conditions, when food is less abundant and individuals are presumably in poorer condition, and also in situations when the cost of performing the aerial display is likely greater, such as in more windy conditions, or when males display while carrying food.

METHODS

Study Areas and Species. We conducted the study from 1997–01 in two study areas in western France, approximately 60 km from each other, where Montagu's Harrier populations had been monitored for 7–10 yr (Millon and Bretagnolle 2008). Marais de Rochefort, hereafter "RO" (45°57'N, 0°55'W), consists of 190 km² of marshlands that have been gradually converted to cereal production over the last 20 yr. Deux Sèvres, hereafter "DS" (46°11'N, 0°28'W), covers 340 km² of intensively farmed land dedicated mainly to cereal production.

Common voles (*Microtus arvalis*) are the most important prey for Montagu's Harriers in the study areas (Salamolard et al. 2000, Millon and Bretagnolle 2008). Breeding numbers and reproduction of Montagu's Harriers in the study areas strongly depend on voles: when voles are abundant, breeding Montagu's Harriers are more numerous, birds are in better condition, breed earlier and more successfully (Salamolard et al. 2000, Millon and Bretagnolle 2008). Population sizes in the study areas during the study years ranged from 14 pairs in 1997 (a low vole year) to 60 pairs in 1999 (a high vole abundance year; Table 1).

Male Montagu's Harriers feed their mates in the pre-laying and incubation periods and contribute 80% of the food for the nestlings from hatching to independence (Arroyo 1995, Arroyo et al. 2004). Montagu's Harriers are sexually dimorphic in plumage (males are light grey, females are brown) and size (males are smaller and lighter than females, Cramp and Simmons 1980). Montagu's Harriers do not defend feeding territories (Arroyo et al. 2004), but they defend an area in a 50–200 m radius around their nest, that we defined as the "breeding territory." Females spend most of the time between pair formation and incubation within this breeding territory. Further details on the species can be found in Cramp and Simmons (1980) and Arroyo et al. (2004).

Display Frequency. We observed behavior of breeding pairs using continuous focal sampling to quantify the occurrence of aerial displays in 1997–98. Study pairs were selected for the ease of observation (good viewing conditions of breeding territory) and if possible for the presence of individuals that could be identified either from plumage traits or from their individual patagial wing-tags (see Mougeot et al. 2001 for further details). Birds were observed with 10 × 42 binoculars at a distance of 200–400 m from study nests, and always seemed

Table 1. Montagu's Harrier breeding population size, mean (\pm SD, and range) number of neighbors and vole abundance estimate (vole/100 trap-nights) in each of the study areas and years.

YEAR AND STUDY AREA ¹	BREEDING PAIRS	NUMBER OF NEIGHBORS	VOLE ABUNDANCE
1997 DS	14	1.1 \pm 1.0 (0–3)	0.38
1997 RO	16	2.0 \pm 1.3 (0–3)	0.22
1998 DS	42	0.8 \pm 1.0 (0–3)	1.90
1998 RO	22	3.7 \pm 1.9 (0–6)	1.42
1999 DS	59	1.3 \pm 1.4 (0–4)	8.20
1999 RO	20	4.1 \pm 2.1 (0–6)	2.48
2000 RO	12	2.5 \pm 0.9 (0–3)	0.77
2001 DS	42	2.1 \pm 2.4 (0–7)	0.70

¹ DS = Deux Sèvres, RO = Rochefort.

unconcerned by the presence of the observer. We conducted a total of 365 observations on 50 breeding pairs, which lasted on average 108 ± 41 min. We recorded all displays performed by the male and female of focal pairs. From these data we calculated male and female display rate as number of displays divided by observation length. Observations took place throughout the day (from 07:00 H to 20:00 H) and throughout the breeding season (from 27 April to 19 August).

In each study area, all nests were located each year and their position was mapped on a GIS (ArcGIS). We used the number of nests within a 600-m radius of each nest as a measure of nest-spacing and colony size (see Arroyo 1995, Arroyo et al. 2001). Monitored birds had 0 to 6 neighbors, covering the range observed in the study areas and years (Table 1). Monitoring of breeding pairs included regular nest visits during the breeding cycle to measure nestlings and accurately estimate laying date (see Arroyo 1995). We assigned *a posteriori* each observation bout with a day number relative to laying onset (day 0 being the day the first egg was laid), as the difference in days between the observation date and the date of laying onset (hereafter called “relative date”).

Display Characteristics. Aerial displays of Montagu's Harriers typically consist of an ascendant flight followed by a rapid downward plunge toward the ground that includes a series of undulations, twists, or loops, accompanied by displaying calls (see Simmons 1991 and Fig. 1). From 1999 to 2001, we conducted specific behavioral observations to record the characteristics of individual aerial displays during the pre-laying period. For each display observed ($n = 96$ in total), we recorded the following: (1) sex of the bird performing it; (2) estimated height from

which it started (range 30–800 m, with a precision of 10 m for altitudes up to 100 m, and 50 m for altitudes above that; estimated heights by different observers were compared to test reproducibility); (3) estimated height at which the display ended (range 300 to 0 m; birds sometimes landed at the end of the display); (4) number of twists performed; (5) number of undulations performed; (6) number of full loops performed (see Fig. 1); (7) number of display calls emitted; (8) whether the individual displaying had prey in its talons or not; and (9) duration (in sec) of the display (timed with a stop watch). Observations were done by single observers, mostly using a voice recorder. From this information we calculated for each display: frequency of loops (as number of loops divided by display duration), frequency of twists, frequency of undulations, frequency of calls, and descending flight speed (as total distance descended: starting height minus height at ending, divided by display duration). We also noted the wind strength, scored as: 0 = no wind; 1 = light wind (0.1–10 km/hr); 2 = strong wind (>10 km/hr).

Vole Abundance. We evaluated common vole abundance in April using live-trapping without marking. Trap-lines consisted of 51 traps in a 100-m transect set for 24 hr in randomly selected fields in different habitats (permanent and annual crops, pastures, 20–36 trap-lines in RO, 80–96 in DS). We calculated vole abundance for each of the study areas and years as the average of capture/100 traps/24 hr among habitat categories, weighted according to their relative surface (Table 1, and see Millon and Bretagnolle 2008 for more details).

Statistical Analyses. We used R version 2.13 (R Development Core Team 2010) for statistical analyses.

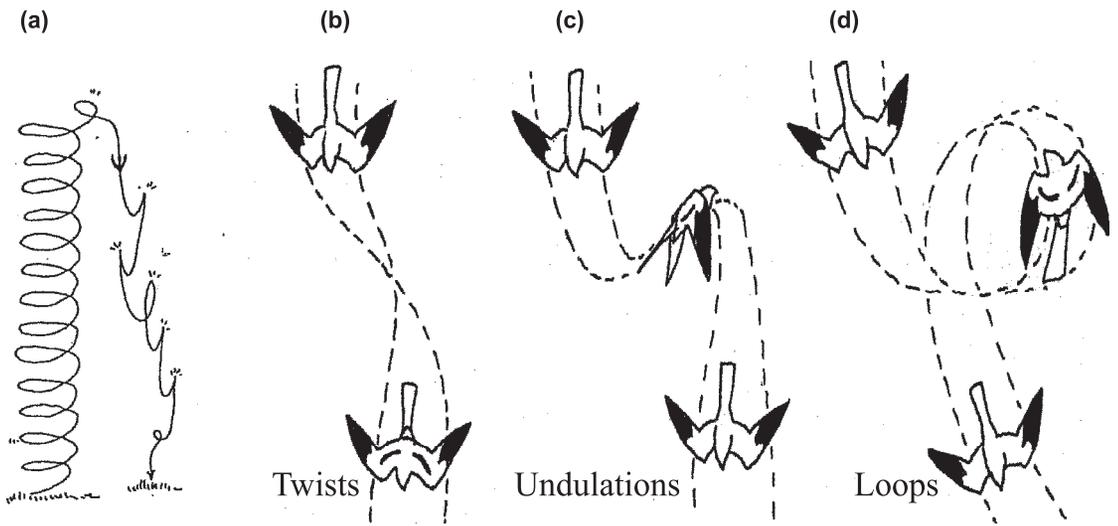


Figure 1. Schematic illustration of the components of a Montagu's Harrier aerial display. Birds circle up to a certain height (a), then plunge to the ground while performing a series of twists (b), undulations (c) or loops (d), and display calls.

We grouped relative date in 5-d periods, and calculated the average observed display rate (displays/hr) for males and females for each 5-d period to describe variation in display frequency throughout the breeding season.

We tested whether male or female display rate varied with colony size (number of neighbors within 600 m) and vole abundance. The dependent variables were log transformed, and effects tested using a GLMM that included the variable "focal pair" as a random effect to account for repeated observations on monitored pairs. We only used observations from the pre-laying period (up to relative day = 4) for this analysis. We selected the model with lowest AICc, comparing the null model, the one with both explanatory variables and the ones with each of the explanatory variables separately.

To summarize aerial displays characteristics, we carried out a PCA with all the following variables: starting height, descending speed, frequency of loops, frequency of undulations, frequency of twists, and frequency of display calls. We tested for between-sex differences in PC scores using ANOVA. For males separately, we subsequently used Generalized Linear Mixed Models (GLM) to evaluate which variables (vole abundance, colony size, wind strength, presence of prey in talons) best explained variation in display characteristics, as summarized by PC scores. PC scores were fitted to models using a Gaussian distribution. "Colony" was included as a

random factor to account for the potential nonindependence of observations in the same colony (as some individuals were not marked, observations in the same colony in different days could belong to the same individual). We performed all possible combinations of the independent variables with the function dredge (library MuMIn) and selected the best models (those within two values of the lowest AICc). We present model-averaged parameter estimates for the variables included in those models, as well as relative weights (Burnham and Anderson 2002). We do not discuss variables for which coefficients included zero, taking into account the standard error. We did not perform similar analyses for females, as we did not have enough variability in our small sample.

RESULTS

Display Frequency. Male and female display frequency varied throughout the breeding season (Fig. 2). Sky-dancing displays were performed by both sexes, and throughout the breeding season, but display frequency was highest in the pre-laying period for both sexes (Fig. 2), when it averaged 0.40 ± 1.11 displays/hr for males (range 0–8), and 0.07 ± 0.28 displays/hr for females (range 0–2). In males, there was a clear peak on display frequency just prior to laying onset, and an apparent one approximately 3 wk before laying (Fig. 2), although sample size at that time was small. Female display

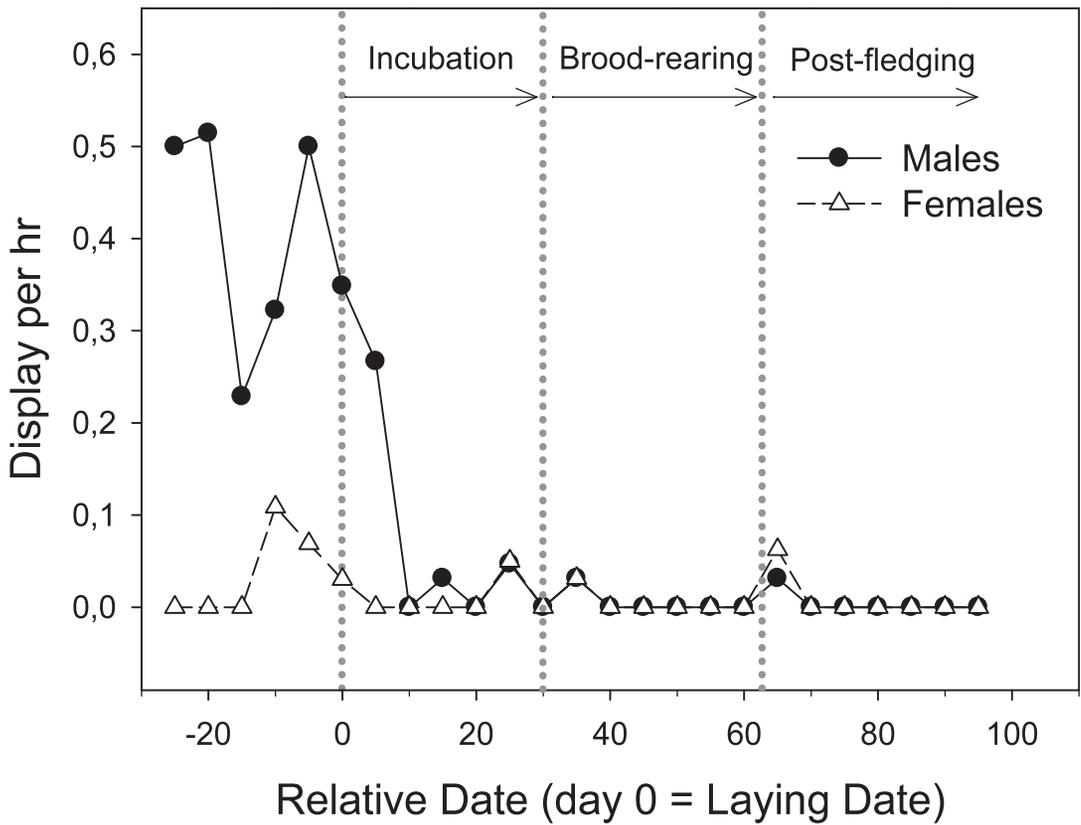


Figure 2. Variation in aerial display frequency by male and female Montagu’s Harriers in relation to the timing of breeding (day 0 = laying onset).

rate also peaked in the pre-laying period (about 10 d before laying onset), but much less markedly than in males. Display frequency by males and females during the pre-laying period increased with colony size (Table 2, model-averaged coefficients: 0.035 ± 0.008 and 0.008 ± 0.003 for males and females respectively, Relative Variable Importance = 1) and with vole abundance (Table 2, model-averaged coefficients: 0.016 ± 0.024 and 0.006 ± 0.010 for males and females respectively, Relative Variable Importance = 0.29). Aerial displays by both sexes

were also observed after laying (Fig. 2), although display frequencies for the incubation, brood-rearing and post-fledging periods for either sex were much lower, averaging between 0.01 ± 0.06 displays/hr (males and females during brood-rearing and post-fledging periods) and 0.05 ± 0.32 displays/hr (males during incubation).

Display Characteristics. Male harrier displays included an average of six twists, three undulations, two loops, and five calls. They typically began at 270 m above the ground, descended down to 20 m

Table 2. Results from the GLMM analysis of frequency of male and female Montagu’s Harrier sky-dancing displays in the pre-laying period in relation to number of neighbors or vole abundance. We show only models with delta AICc < 2.

MODEL	MALES			FEMALES		
	AICc	DELTA	WEIGHT	AICc	DELTA	WEIGHT
No. of neighbors	-60.91	0.00	0.71	-269.56	0.00	0.71
No. neighbors + vole abundance	-59.08	1.83	0.29	-267.74	1.82	0.29

Table 3. Average characteristics of sky-dancing aerial displays of male and female Montagu's Harriers, mean ± SD, with range in brackets.

CHARACTERISTICS	FEMALES (n = 15)	MALES (n = 81)
Starting height (m)	213 ± 145 (100–500)	271 ± 193 (30–800)
Final height (m)	60 ± 83 (5–300)	21 ± 29 (0–150)
Length (sec)	90 ± 47 (30–180)	122 ± 120 (30–780)
Speed (m/sec)	2.2 ± 1.1 (0.8–4.8)	2.9 ± 2.0 (0.4–9.7)
Twists	2 ± 2 (0–7)	6 ± 6 (0–30)
Undulations	2 ± 1 (0–4)	3 ± 6 (0–31)
Loops	0 ± 0 (0–1)	2 ± 2 (0–12)
Calls	1 ± 2 (0–5)	5 ± 4 (0–20)

on average (sometimes ending on the ground), and involved descending flight speeds that ranged from 0.4 to 9.7 m/sec (Table 3). Female displays typically started from lower heights, ended higher above the ground, were slower and included fewer loops, twists or undulations than those of males (Table 3).

The Principal Component Analysis (PCA) conducted on recorded display characteristics identified three axes with eigenvalues >1, which explained 83.9% of variation (Table 4). The first axis correlated positively with all display parameters: it identified displays that started at higher altitude, descended at higher speeds, with higher frequencies of twists, undulations, loops, and with more displaying calls. It thus characterized the overall complexity and “intensity” of the display. The second axis opposed faster displays that started from a higher altitude, but had a low complexity (in term of twists and undulation frequency) to displays that were slower, started from lower altitude, but were more complex. The third axis contrasted displays with more loops than undulations to others with more undulations than loops.

Table 4. Results from the Principal Component Analyses conducted on aerial display characteristics (n = 96 displays).

VARIABLES	PC1 ¹	PC2 ²	PC3 ³
Call frequency	0.541	0.282	0.121
Twist frequency	0.525	0.284	-0.012
Undulation frequency	0.190	0.245	-0.682
Loop frequency	0.418	-0.117	0.593
Starting height	0.212	-0.655	-0.312
Descending speed	0.419	-0.465	-0.266

¹ Eigenvalue 2.41, proportion of deviance explained 0.40.

² Eigenvalue 1.50, proportion of deviance explained 0.25.

³ Eigenvalue 0.12, proportion of deviance explained 0.19.

PC1 scores significantly differed between sexes ($P = 0.002$), with males having more complex and intense displays than females (Table 3, Fig. 3). In contrast, PC2 and PC3 scores did not differ significantly between sexes ($P = 0.37$ and $P = 0.15$, respectively). Overall, scores of female displays were within the range of those of male displays, but had much lower variability (for all PC axes) and were within the lower range of that observed for male displays (for PC1).

Variation in male PC1 scores was explained mostly by vole abundance and prey handling (Table 5). Displays were more intense (higher PC1 values) when voles were more abundant, but were less intense when males displayed while carrying prey (Table 6, Fig. 4).

Variation in PC2 scores in males was explained by number of neighbors, vole abundance, and wind conditions (Table 5). Displays started from higher and were faster with increasing number of neighbors and more abundant voles, and also when there was no wind. With increasing wind speed, both height and descending speed decreased, but displays were relatively more complex (more twists and undulations; Table 6). PC3 increased with wind speed and number of neighbors: displays tended to have more loops instead of undulations in more windy conditions and in larger colonies (Table 5, 6).

Females never displayed with prey in their talons. Additionally, most displays were observed when there was no wind (87%, $n = 15$), the remainder in light wind conditions.

DISCUSSION

Our results support the hypothesis that Montagu's Harrier sky-dancing displays, particularly the most elaborate ones, are costly to produce, and

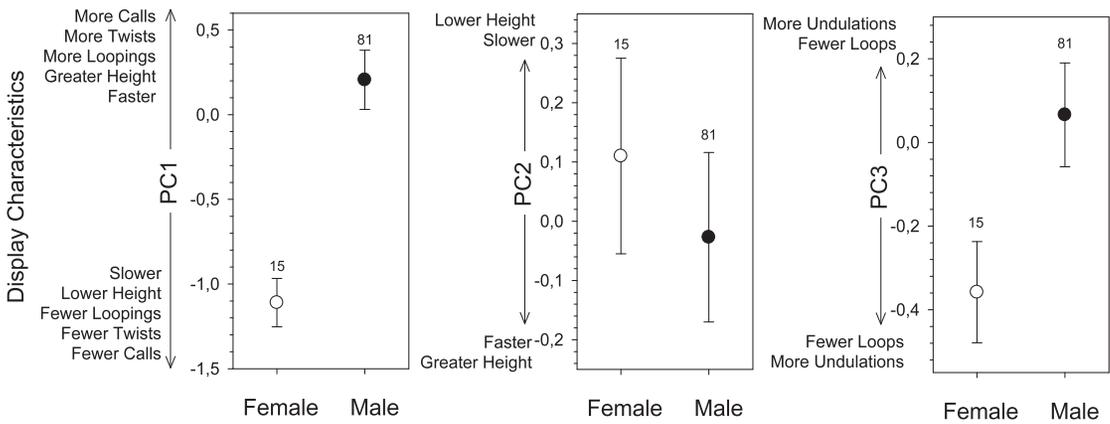


Figure 3. Sexual dimorphism in display characteristics of Montagu’s Harriers, as summarized by average (\pm SE) PC scores. Filled symbols: male aerial displays; open symbols: female aerial displays. Sample sizes are given above error bars.

may thus potentially honestly advertise individual quality. Our observations also were consistent with the hypothesis that these displays, performed most frequently during the pre-laying period, have both intra- and intersexual functions.

Displays, Mate Choice, and Sexual Competition.

As expected, males displayed more frequently and performed more elaborate sky-dancing displays than females, which is consistent with female-based mate choice. Male display frequency was high 3 wk before laying, corresponding roughly with arrival time on the breeding grounds (Arroyo 1995) and thus the time of pair formation. This suggests that these displays may be used to attract mates and to

facilitate mate appraisal and choice, as has been suggested in other harriers (Simmons 1988).

The “aerial display hypothesis” suggests that sexual selection favors aerial agility, and hence small size, in species with male display flights. Such a relationship has been found in Dunlins (*Calidris alpina*), where smaller males performed more, and more costly display flights than larger males (Blomqvist et al. 1997). The fact that Montagu’s Harrier males are lighter and more agile than females (Cramp and Simmons 1980) may be related to sexual selection favoring aerial agility in this species, also supporting that sky-dancing displays in Montagu’s Harriers may be used for mate choice.

Table 5. Results of the GLMM analyses conducted to select the best models explaining variation in aerial display characteristics of male Montagu’s Harriers (PC scores; Table 4). In the table, we present only models with delta AICc <2.

AXIS	MODEL	AICc	DELTA	WEIGHT
PC1	Vole abundance	310.33	0.00	0.22
	(null)	310.38	0.05	0.22
	Vole abund. + prey	310.99	0.67	0.16
	Wind	311.58	1.25	0.12
	Prey	311.93	1.60	0.10
	Vole abund. + wind	312.15	1.82	0.09
	No. neighbors	312.24	1.91	0.09
PC2	No. neighbors + vole abund.	255.88	0.00	0.35
	No. neighbors + vole abund. + wind	256.61	0.73	0.24
	No. neighbors + wind	256.61	0.90	0.22
	No. neighbors	257.07	1.19	0.19
PC3	Wind	252.93	0.00	0.41
	(null)	254.16	1.23	0.22
	No. neighbors + wind	254.38	1.46	0.20
	Vole abund. + wind	254.64	1.71	0.17

Table 6. Model-averaged coefficients (and their standard error) of the variables included in the models shown in Table 3. Variables highlighted in italics have coefficient estimate \pm SE that include zero. Also shown is the Relative Variable Importance (the sum of the weights of the models in which that variable was included; Burnham and Anderson 2002).

AXIS	EXPLANATORY VARIABLES	COEFFICIENT	SE	RELATIVE VARIABLE IMPORTANCE
PC1	Vole abundance	0.123	0.077	0.47
	Prey (yes)	-0.528	0.500	0.26
	<i>Wind strength</i>	-0.217	0.255	0.21
	<i>Number of neighbors</i>	0.061	0.103	0.09
PC2	No. of neighbors	-0.259	0.115	1.00
	Vole abundance	-0.192	0.057	0.59
	Wind strength	0.252	0.179	0.46
PC3	Wind	0.320	0.176	0.78
	No. of neighbors	0.132	0.099	0.20
	<i>Vole abundance</i>	-0.032	0.043	0.17

This would need to be tested by evaluating whether display frequency or quality are related to male size, and whether the latter is in turn related to higher aerial agility and foraging ability, and therefore to fitness.

Sky-dancing frequency also peaked just prior to and during laying, which corresponds to the females' fertile period (Mougeot et al. 2001, 2006). Extra-pair copulations occur in many raptors, and there is a risk that these result in extra-pair fertilization when

females are fertile (Mougeot 2004). Male Montagu's Harriers may use more frequent copulations, mate guarding, and aggression to ensure their paternity (Mougeot et al. 2001). The high sky-dancing frequency during this time, when social mate choice is already made, suggests that mate defense (and thus intrasexual competition) is a more likely function at this time. Indeed, when a male decoy was presented close to their females during the fertile period (in order to simulate a territorial intrusion), male

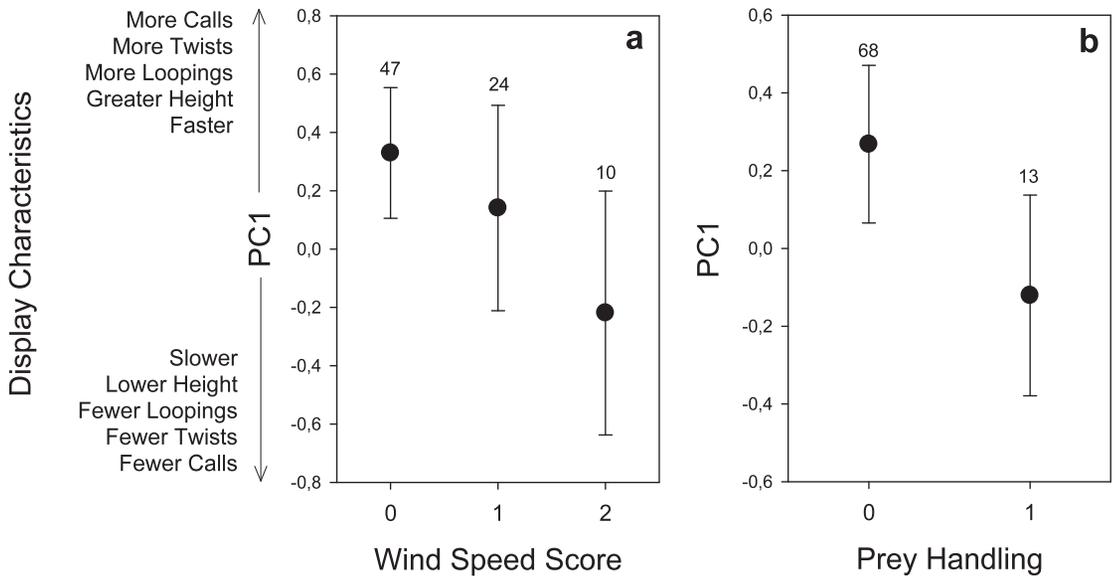


Figure 4. Average (\pm SE) PC1 scores of male Montagu's Harrier aerial displays in relation to wind strength (see methods) and prey handling (0 = no prey; 1 = displaying while carrying prey). Sample sizes are given above error bars.

Montagu's Harriers responded by performing more sky-dancing displays (Mougeot et al. 2001).

Additionally, both male display frequency in the pre-laying period and display characteristics (specifically those described by PC2 and PC3) also varied with colony size. Displays at larger colonies started higher and were faster (lower PC2 scores) but had more loops and fewer undulations (higher PC3 scores). This is consistent with a sexual function, as both levels of inter- and intrasexual competition typically increase with colony size (Arroyo et al. 1999, Mougeot 2004).

Frequency of sky-dancing in females also increased with colony size. This may indicate that competition among females for mates is also greater at larger colonies, and that there may be reciprocal mate choice (male choice of females), as has been suggested in other monogamous birds (Amundsen et al. 1997, Martínez-Padilla et al. 2011). However, their lower frequency and overall lower complexity and variability than those of males suggests that either the intensity of male choice by females is lower than the reciprocal, or that it is mainly based on other traits, such as age or experience.

Costs of Displays in Males. Analyses of factors affecting the characteristics of sky-dancing displays or their frequencies also revealed some costs of performing these displays, which indicates their potential for indicating individual quality. For example, male display "intensity," as observed by the variation in PC1 scores, decreased when displays were performed with prey in the talons, and prey carrying is known to be a handicap for flying birds (Hedenstrom and Alerstam 1995). PC2 was explained by wind conditions, suggesting that display height and speed are impaired by wind, but males may "compensate" in windy conditions by trying to increase the complexity of the display. PC3 in males also was explained mainly by wind, but in this case windy conditions were associated with a higher relative frequency of loops versus undulations. Loops are more difficult to perform than simpler undulations, so this result suggests that wind may help to perform these loops, or else that performing loops in windy conditions is a way to advertise quality.

We also found a relationship between vole abundance and both male sky-dancing frequency and characteristics (PC1 and PC2). This was also consistent with the hypothesis that these displays are energetically costly. Condition-dependent signals are easier to produce in years or sites when food is more abundant or when individuals are in better

nutritional condition. The fact that the relationship with display frequency was weak may be related to the low variability within our sample: display frequency was sampled only in two years of low and intermediate vole abundance, respectively (Table 1). Sky-dancing displays in 1996 or 1999, two peak vole years (Millon and Bretagnolle 2008, and Table 1), although not quantified, were very common (B. Arroyo, F. Mougeot, and V. Bretagnolle unpubl. data). Similar relationships between food abundance or availability and thus harrier nutritional condition and display frequency have been found for other harriers (Simmons 1988, 1991).

Synthesis and Perspectives. Our observations were consistent with the hypothesis that sky-dancing displays are costly and have both intra and intersexual functions. However, results also suggested that sky-dancing displays serve functions beyond those stated here, because they occur beyond the pre-laying period and even after fledging. Additionally, harriers exhibit many other types of aerial displays, which may have both sexual and non-sexual functions (Pandolfi and Pino d'Astore 1994, Pandolfi 1996). Further studies could expand the range of displays analyzed.

Regarding the sexual function of sky-dancing displays, future work should identify how honest these costly signals are, and whether the frequency or complexity of displays advertise other male quality traits, such as hunting ability (Simmons 1988). For that, we should investigate whether individuals doing the most costly displays are those with better phenotypic quality, or the best food providers, and whether displays have fitness consequences (e.g., reducing mate choice time, advancing laying date or being related to higher reproductive rate or better nestling condition).

Different raptor species also perform very different aerial displays (Ross 1941, Jepsen 1986, Pandolfi and Barocci 1994, Debus 1995). In future works, comparative analysis could be used to relate characteristics of raptor aerial displays to other species-specific characteristics such as body shape and wing-loading, or diet and the ability to hunt certain prey types, and evaluate whether these characteristics influence the relative costs of different displays.

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