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EXPLORING THE INFLUENCE OF URBANIZATION ON MORPH DISTRIBUTION AND MORPH-SPECIFIC BREEDING PERFORMANCE IN A POLYMORPHIC AFRICAN RAPTOR

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ABSTRACT.—Global urbanization is rapidly increasing, specifically within Africa. However, the effects of these processes on Africa's wildlife are largely unexplored. For many species, the effects are detrimental, whereas others are able to colonize these human-altered environments and can even thrive. Raptors are positioned at the top of the food chain and therefore particularly susceptible to environmental changes, and yet they are increasingly associated with urban areas. Given that adaptations to cope with urban stressors may differ from those occurring in more natural habitats, we might expect that directional selection in urban areas could account for phenotypic divergence between urban and rural individuals. This might include selection for different plumage coloration, which could be facilitated in color polymorphic species because no additional mutations are required to create variation. Color polymorphism is common in raptors, with 22% of the *Accipitridae* family being polymorphic. In this study, we focus on Black Sparrowhawks (*Accipiter melanoleucus*) in Cape Town, South Africa. We explore whether the morphs are distributed differently along an urban–rural gradient and thus show a local adaptation. Using a long-term study (16 yr), we also investigate whether morph was related to the timing of breeding and breeding performance along the urban gradient. We found no differences of the morph distribution or of their breeding performance in relation to levels of urbanization. Our study represents the first to examine the breeding distribution of a polymorphic raptor in relation to urbanization and one of the first to explore avian productivity in relation to urbanization in Africa.

KEY WORDS: *Black Sparrowhawk*; Accipiter melanoleucus; *breeding*; *coloration*; *morph*; *polymorphism*; *reproductive rate*; *South Africa*; *urban ecology*.

EXPLORANDO LA INFLUENCIA DE LA URBANIZACIÓN EN LA DISTRIBUCIÓN DE MORFOS Y LA REPRODUCCIÓN DE CADA MORFO EN UNA RAPAZ POLIMÓRFICA AFRICANA

RESUMEN.—La urbanización a nivel mundial está creciendo rápidamente y específicamente en África. Sin embargo, los efectos de estos procesos sobre la vida silvestre africana no son conocidos. Para muchas especies, los efectos son perjudiciales, mientras que otras son capaces de colonizar estos ambientes modificados por el hombre e incluso pueden prosperar. Las aves rapaces están posicionadas en la cima de la cadena alimenticia y por lo tanto son particularmente sensibles a los cambios ambientales; no obstante, cada vez se las asocia más con áreas urbanizadas. Dado que las adaptaciones para afrontar los factores de estrés urbanos pueden diferir de los que se presentan en hábitats más naturales, podríamos esperar que la selección direccional en áreas urbanas sea responsable de la divergencia fenotípica entre individuos urbanos y rurales. Esto puede incluir la selección de coloraciones de plumaje diferentes, que puede verse facilitada en especies que presentan polimorfismo cromático, ya que no son necesarias mutaciones adicionales para crear esta variación. El polimorfismo cromático es común en las rapaces, donde el 22% de los integrantes de la familia *Accipitridae* lo poseen. En este estudio, nos centramos en *Accipiter melanoleucus* en la Ciudad del Cabo, Sudáfrica. Estudiamos si los morfos se distribuyen de manera diferencial a lo largo de un gradiente urbano-rural y por tanto evidencian una adaptación local. Utilizando un estudio a largo plazo (16 años), también investigamos si el morfo estuvo relacionado con los tiempos de cría y el resultado de la reproducción a lo largo del gradiente urbano. No encontramos diferencias en la distribución de los morfos o del resultado de la reproducción en relación con los niveles de urbanización. Nuestro estudio es el primero en examinar la distribución reproductiva de una rapaz polimórfica en relación con la

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urbanización y una de las primeras en explorar la productividad de las aves en relación con la urbanización en África.

[Traducción del equipo editorial]

Globally, more people live in urban areas than in rural ones. Africa and Asia are urbanizing faster than any other region in the world. By 2050, 66% of the world's population is projected to be urban (United Nations 2015). As the global human population continues to grow, the area of urban land cover also increases, and natural habitats are transformed into human-altered ecosystems. This rapid urbanization has profound environmental consequences, including declines in biodiversity (Marzluff 2001, McKinney 2006, Shanahan et al. 2014). However, some species can take advantage of the new habitat and the altered patterns of predation and competition that are associated with a shift in the composition of species assemblages (Catterall 2009). It is now widely acknowledged that species respond to urbanization in three distinct ways: They can either "avoid," "adapt" to, or "exploit" urban areas (Blair 1996, Blair 2001, McKinney 2006, Shochat et al. 2006, Kark et al. 2007).

Raptors are particularly vulnerable to anthropogenic disturbance due to their slow life-history (i.e., late onset of maturity, low fecundity) and are important indicator species for ecosystem-wide processes due to their position at the top of the food chain (Newton 1979). Although species richness of carnivores tends to decrease in urbanized areas (Reis et al. 2012), several raptor species appear to benefit from urbanization (Love and Bird 2000). Typically, specialized diurnal raptors suffer from increasing urbanization, but those benefitting from an increased biomass of avian prey (Rutz 2008, Suri et al. 2017) or generalists appear to be less affected and can even thrive in these environments (Sorace and Gustin 2009).

Urbanization can expose populations to diverse environments with different selective pressures (McKinney 2006) that can result in different adaptations. For example, this might operate on behavioral traits in a way that selection in urban habitats might favor bolder exploratory behaviors in birds (i.e., risk-taking [Bókony et al. 2012] and boldness [Atwell et al. 2012]), or it could act on plumage coloration, for example, if certain plumage colors provide adaptation to cope better with elevated pollution or parasite risk associated with urban living (Jacquin et al. 2011). Such associations can stem from pleiotropic effects of the genes regulating the synthesis of eumelanin in vertebrates (Ducrest et al. 2008). The different selection pressures in urban areas could therefore lead to directional selection and phenotypic divergence between urban and rural individuals (Luniak 2004).

Polymorphic species may be better adapted to cope with the challenges of environmental change or may be able to expand their ranges more quickly into novel environments, because selection pressure can act on a pre-existing trait that may be beneficial in new conditions. In fact, color polymorphism is associated with lower extinction risk in birds in some cases (Ducatez et al. 2017). In addition, overall color polymorphic species are evolutionarily older than monomorphic ones, which may explain why they may be more resistant to stress (Cattin et al. 2016, but see also Hugall et al. 2012). Differential color patterns can influence performance and fitness of individuals under varying environmental conditions through both direct effects of pigment production (e.g., camouflage or thermoregulation) and indirect effects (e.g., suites of correlated physiological and behavioral traits; see review in Roulin 2004 and Ducrest et al. 2008). Color polymorphism is relatively rare in birds (3.5% of species; Galeotti et al. 2003), but is more common in raptors, with 22% of the Accipitridae family being polymorphic (Galeotti et al. 2003). Color variation can be discrete (e.g., Black Sparrowhawks [*Accipiter melanoleucus*] occurring as either dark or light-morph adults [Amar et al. 2013]) or continuous (e.g., Tawny Owls [*Strix aluco*] or Common Buzzards [*Buteo buteo*]; Brommer et al. 2005, Ulfstrand 1977). Morph type is known to covary with several behavioral and physiological traits (Roulin 2004), as well as immune and stress responses (Lei et al. 2013, Saino et al. 2013), which could be beneficial in an urban environment. Thus, urbanization may exert selection pressure differentially on morphs of the same species. For example, elevated pollution during the Industrial Revolution induced a novel selection pressure in industrial areas through differential background crypsis and predation risk for different morphs of the peppered moth (*Biston betularia*; "industrial melanism;" Kettlewell 1955). Similarly, urban Rock Pigeons (*Columbia livia*) tend to be darker than their rural counterparts, which was associated with higher stress

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exposure in the city that favors darker coloration (Johnston and Janiga 1995, Jacquin et al. 2011). Beyond the improved ability of darker morphs to cope with pollutants (Chatelain et al. 2014) and stress (Almasi et al. 2012), they might also have higher resistance against diseases and parasites (e.g., Jacquin et al. 2011, Lei et al. 2013). Additionally, darker juvenile Rock Pigeons in Paris showed higher survival rates than lighter individuals (Récapet et al. 2013), potentially due to their higher competitiveness and their ability to access more food resources (Récapet et al. 2013), and darker Eurasian Siskins (*Spinus spinus*) also show increased aggression and dominance (Senar 2006).

Additionally, different morphs may be adapted to different environments. For example, color-dependent habitat choice on a small scale is known from Barn Owls (*Tyto alba*), in which reddish females bred in sites with more arable fields and less forest than whitish females (Dreiss et al. 2012). Among Pacific Reef-Egrets (*Egretta sacra*), dark morphs forage preferentially in shaded streams (Rohwer 1990) where white morphs are largely absent. Likewise, light-morph Red-tailed Hawks (*Buteo jamaicensis*) use open perch sites and dark morphs use more dense cover (Preston 1980). All three studies provide evidence that polymorphic species chose their foraging grounds according to land-cover type and/or light levels that best conceal them from their prey.

In this study, we explore this question of how morphs vary with urbanization in the Black Sparrowhawk, a polymorphic raptor that colonized the area of Cape Town, South Africa, in the last two decades. Black Sparrowhawks appear to have adapted well to urban areas, with more than 50 breeding pairs (Martin et al. 2014b) within our study area and no obvious negative health effects on their offspring (Suri et al. 2017) or their reproductive rates (Rose et al. 2017). In South Africa, morph frequencies vary from east to west along a clinal gradient following winter rainfall patterns (Amar et al. 2013, 2014) and the intensity of solar radiation (Tate et al. 2016b). In the western part of the range, approximately 80% of the population are dark morphs, whereas in the eastern part the reverse is observed, with dark morphs accounting for roughly 20% (Amar et al. 2013). The higher percentages of dark morphs in the west may be associated with a greater resistance to blood parasites (Lei et al. 2013) and improved foraging success under greater cloud cover in the winter rainfall regions coinciding with their breeding season (Tate et al. 2016b).

Here we explore the influence of urbanization on the breeding distribution, timing of breeding, and breeding performance of the different Black Sparrowhawk color morphs. The morphs of this species might also be expected to be distributed differently relative to levels of urbanization, as they are known to use different environments for hunting, with dark morphs foraging in more closed habitats (Tate and Amar in press). Therefore, based on the possibility of pleiotropic effects linked to eumelanin production (Ducrest et al. 2008), we might predict dark morphs to exploit more urbanized areas than light morphs. In contrast, based on morph-specific foraging behavior (Tate et al. 2016b, Tate and Amar in press), we might predict dark morphs to occupy less urbanized areas (more trees, darker conditions), and expect light morphs to be in more urbanized areas, with less tree cover.

Based on these opposite expectations for habitat selection, we further predict that the timing of breeding may be earlier and breeding performance may be higher in any favored habitat. However, because no negative effects on individual health, including blood parasites (Suri et al. 2017), or breeding performance (Rose et al. 2017) are known in relation to urbanization in this population, we expect morph distribution to be more closely related to foraging behavior than to a potential adaptive function of eumelanin.

We also extend this question by looking at the pair morph combination, which has previously been shown to influence breeding performance (Tate et al. 2016a), offspring survival, and recruitment rates (Sumasgutner et al. 2016c). Here our predictions are similar for pairs made up of the same morphs (i.e., all-dark pairs to be in more urbanized environments and all-light pairs to be in less urbanized environments based on pleiotropic effects of producing eumelanin, and the opposite based on their foraging behavior). For mixed pairs, we might expect pairs to be in more intermediate levels of urbanization, or may expect the influence of habitat to be most closely associated with the male's morph. Males have a greater role in nest-site selection and food provisioning, as they provide most of the food during incubation and also during the nestling-rearing period (Katzenberger et al. 2015).

Methods

Study System and the Urban Gradient. This study focused on the resident population of Black Sparrowhawks on the Cape Peninsula, Western

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Cape, South Africa. The study area, approximately 595 km^2 in size (Martin et al. 2014a), covers various landscapes including heavily urbanized areas (Rose et al. 2017, Suri et al. 2017). Quantification of the urban gradient for each nest site was based on a circular buffer with a radius of 2000 m assigned to each nest. The chosen scale was based on previous work that quantified home-range sizes during the breeding season from adult males fitted with GPS tags (Sumasgutner et al. 2016b). Urban cover was calculated based on 72 different land-cover classes at a 30-m resolution from the 2013–2014 South African National land-cover dataset provided by the Department of Environmental Affairs (Rose et al. 2017). Percentage urban cover (sealed, unproductive areas of land) was derived for each nest buffer using the packages raster (Hijmans and Van Etten 2014), sp (Pebesma 2004) and rgdal (Bivand et al. 2014) in R studio (R Core Team 2016).

Between 2000–2015, systematic monitoring by a team of experienced researchers occurred during the breeding season from March to November. We located territories (Fig. 1) by surveying suitable stands of trees. We confirmed occupancy by indicators such as calling, excreta, prey remains, or nest structures.

Following confirmation of breeding attempts (i.e., incubation behavior was observed), we monitored pairs approximately weekly. Adults occur in either a light or a dark morph, defined by the color of the underwing, breast and belly (Amar et al. 2013), and the morph of each sex was recorded where possible. About 90% of the population is color-ringed, allowing identification of many breeding pairs (see Martin et al. 2014b for further details). We ringed nestlings when they were 3.5–4.5 wk old (Katzenberger et al. 2015). We estimated the age of nestlings visually by the extent of wing and tail feather growth (using reference photographs from nest cameras). This population breeds mainly during the winter months, which coincides with the rainy season (Amar et al. 2014, Martin et al. 2014b). We determined the "lay month" (the month when eggs were laid) by backdating from the age of the nestlings for successful nests (i.e., produced at least one 3.5-4.5-wk-old nestling) and using the incubation behavior (i.e., female sitting low on nest) for unsuccessful nests. We treated lay month as a continuous variable ranging between 1 = January and 12 = December (Martin et al. 2014b). We used three measures of breeding performance as follows: (1) "productivity" was the number of nestlings fledged (0–3 per nest) from all breeding attempts, (2) "brood size" only includes successful nests (1–3 young that fledged per nest), and (3) "breeding success," which we defined as a binomial variable distinguishing between successful and unsuccessful nests.

Statistical Analysis. We analyzed variables relative to urbanization using Generalized Linear Models (GLMs) for morph distribution, multinomial logit models for pair morph combinations, Linear Mixed Models (LMMs) for the timing of breeding and Generalized Linear Mixed Models (GLMMs) for breeding performance, with the packages mlogit (Croissant 2013), nlme (Pinheiro et al. 2014), lme4 (Bates et al. 2015), MASS (Venables and Ripley 2002), lattice (Deepayan 2008), ggplot2 (Wickham 2009), effect displays (Fox 2003), and car (Fox and Weisberg 2011). We scaled all quantitative variables (lay month and urban gradient) in order to bring continuous variables to comparable dimensions to interpret effect sizes for interaction terms. We tested the dispersion of our response variables using the "qcc.overdispersion.test" in the qcc package (Scrucca 2004). Residual distributions of the models were inspected visually to assess model fit.

Morph distribution relative to urbanization. We tested the breeding distribution of different color morphs (response variable, factor in two levels: "dark" and "light") along the urban gradient by fitting a GLM with a binomial error structure and the degree of urbanization as explanatory variable. We used only morph data from color-ringed individuals, or individuals clearly identifiable due to distinct plumage patterns, resulting in a data set of 82 male and 78 female adult sparrowhawks (males: $n = 65$ dark, $n = 17$ light morph; females: $n = 55$ dark, $n = 23$ light morph; Fig. 2). In this specific analysis, we did not use repeated measurements. Thus, no random terms were fitted (i.e., every individual occurs only once in the analyses). When individuals changed nest location within or between years (see multiple nests on territories in Sumasgutner et al. 2016a), or on the rare occasion that individuals changed territory (site and mate fidelity is high; Martin et al. 2014a), we used a mean urban score. Additionally, we explored the distribution of pair combinations along the urban gradient (♀dark–♂dark, ♀dark–♂light, ♀light–♂dark, and ♀light–♂light pairs) using a multinomial response variable (factor in four levels) and again the mean urban score as explanatory variable. We report *Z*- or *t*-values respectively for

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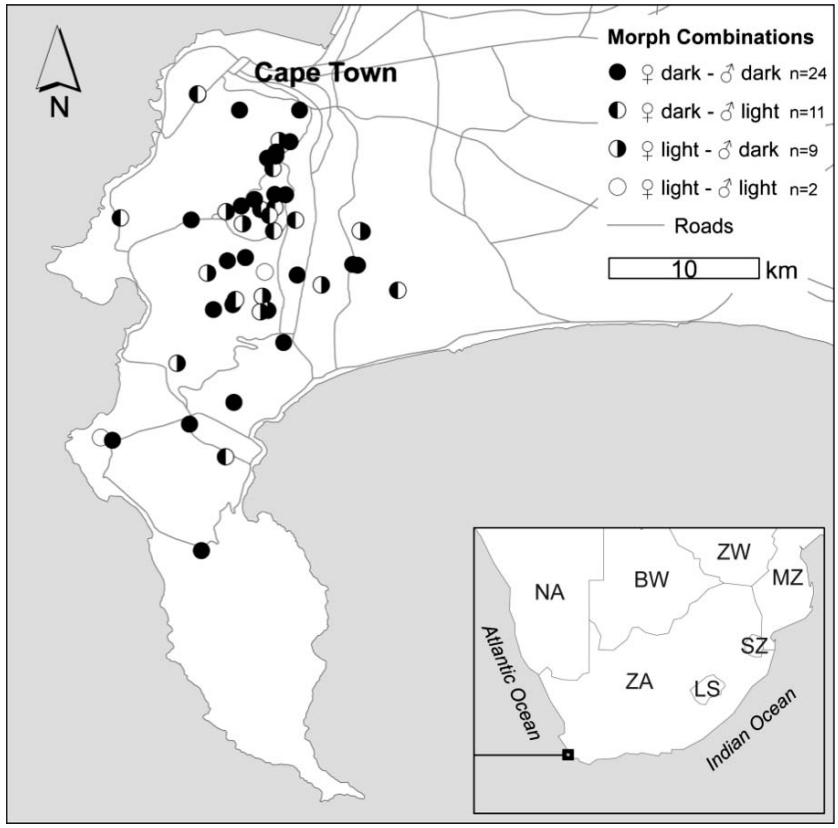

Figure 1. Distribution of Black Sparrowhawk nest localities and the morph combinations of breeding adults in 2015.

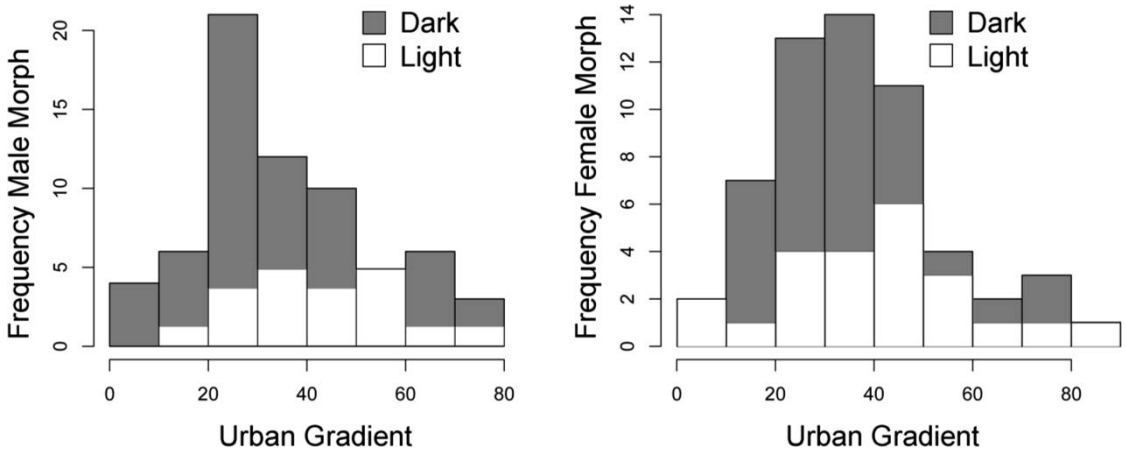

Figure 2. Frequency of different color morphs along the urban gradient (% urban cover) in Black Sparrowhawks. Left panel: males ($n = 82$); right panel: females ($n = 78$).

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Table 1. GLMs investigating the relationship between Black Sparrowhawk morph type (binomial response for males and females, multinomial response for pair morph combinations) and the percentage of urban cover (explanatory variable). The symbols † and ‡ indicate that dark morph and ♀dark–♂ dark pairs, respectively, ($n = 115$) were used as reference levels.

MODEL	RESPONSE	n	df	ESTIMATE	SE	Z/t	P	SIGNIFICANCE[a]
Males	morph†	82	80	0.021	0.015	1.388	0.165	
	(intercept)			−2.175	0.687	−3.168	0.002	**
Females	morph†	78	76	0.015	0.014	1.076	0.282	
	(intercept)			−1.455	0.607	−2.395	0.017	*
Pairs	morph combination‡	200	196					
	♀dark–♂light	28		0.018	0.011	1.591	0.112	
	♀light–♂dark	47		0.009	0.009	0.961	0.337	
	♀light–♂light	10		−0.018	0.020	−0.913	0.361	
	♀dark–♂light (intercept)			−2.085	0.491	−4.246	0.000	***
	♀light–♂dark (intercept)			−1.222	0.387	−3.155	0.002	**
	♀light–♂light (intercept)			−1.855	0.684	−2.714	0.007	**

[a] Significance codes: *** indicates $P < 0.001$; ** indicates $P < 0.01$; * indicates $P < 0.05$.

binomial and multinomial GLMs and for the latter, the corresponding *P*-values (Table 1).

Morph-specific timing of breeding and breeding performance. The overall sample size in all following analyses was 456 breeding attempts surveyed over 16 yr. For these analyses, we used mixed models, with year, territory ID, and nest ID fitted as random terms to account for pseudoreplication arising from same nests sampled repeatedly in multiple years, breeding pairs occupying territories over several years, and multiple measures from different nests within the same year. For the timing of breeding analyses, the lay month (Gaussian distribution) was modeled as the response variable with individual morph or morph combination in interaction with the urban gradient as explanatory variables. For the other analyses examining all three measurements of breeding performance, we accounted for the timing of breeding (using lay month) and explored the interaction of individual morph or morph combination with the urban gradient. Error structures for the GLMMs were negative binomial (to account for overdispersion in our productivity data), Poisson (brood size), and binomial (breeding success). We conducted all analyses (urban gradient × morph interaction) for each sex (different sets of analyses and sample sizes for males and females) and for their pair combination separately. We report χ^2 and *P*-values in the results section based on an ANOVA Table of Deviance using Type II Wald χ^2 tests to test the overall significance of the categorical variable (morph or pair combination; Appendix).

The University of Cape Town's Science Faculty Animal Ethics Committee approved all the procedures used in this study (permit number: 2012/V37/AA). All necessary permits for the monitoring, capturing, and ringing of birds were acquired from CapeNature and South African National Parks.

RESULTS

We found no difference in urbanization levels of territories between the morphs for either males ($\chi^2 = 1.94$, $P = 0.164$) or females ($\chi^2 = 1.27$, $P = 0.280$) or for the pair combination ($\chi^2 = 4.35$, $P = 0.23$; Table 1, Fig. 3). Thus, there was no indication that the different morphs were spatially distributed differently relative to the percentage of urban cover.

When examining the lay month in relation to morph and urbanization levels, we found dark-morph males bred significantly earlier in the season than light-morph males ($\chi^2 = 8.14$, $P = 0.004$), but lay month did not vary according to urbanization levels (Appendix). Similarly, for pair combinations, pairs with a dark-morph male (♀dark–♂dark and ♀light–♂dark) bred significantly earlier than pairs with a light-morph male (♀dark–♂light and ♀light–♂light) ($\chi^2 = 10.34$, $P = 0.016$), but pair combination was not influenced by the urban gradient (Appendix). Lastly, when examining the breeding performance of the morphs in relation to urbanization separately for each sex and for the pair combination, we found no significant interaction between morph and urbanization for productivity, breeding success, or brood size (Appendix). However, in all three analyses, productivity and breeding success were influenced by lay month, with improved breeding performance observed for birds breeding earlier in the season. Brood size was unrelated to lay month.

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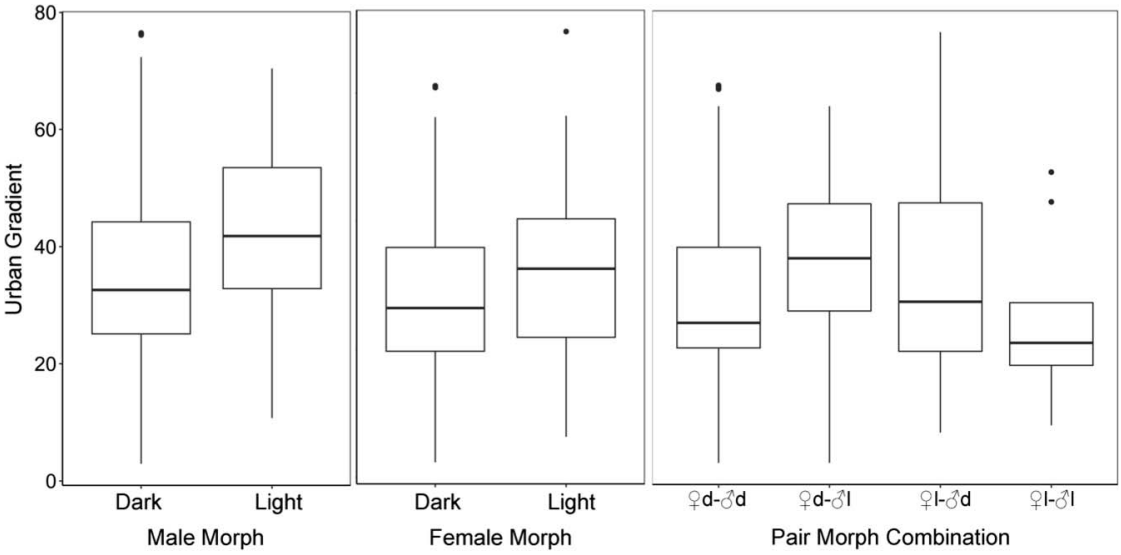

Figure 3. Distribution of morphs for adult males ($n=82$), females ($n=78$), and their pair combination (♀ dark–♂ dark, $n=115$; ♀ dark–♂ light, $n=28$; ♀ light–♂ dark, $n=47$; ♀ light–♂ light, $n=10$), along an urban gradient (% urban cover). Model details in Table 1.

DISCUSSION

We found no support for the hypothesis that different morphs may have a selective advantage corresponding to levels of urbanization. Contrary to our prediction, we found no relationship between the breeding distribution and breeding performance of the different morphs in relation to urbanization. We had predicted that light morphs would occur in more urbanized areas because they are known to forage in more open habitat types (Tate and Amar in press). However, our prediction on the distribution of the morphs was based on the assumption that the two morphs distribute themselves according to an ideal free distribution ("ideal free" or "Fretwell-Lucas model;" Fretwell and Lucas 1969), whereas in fact it is highly likely that intraspecific and interspecific competition limits access to ideal breeding sites (Chalfoun and Schmidt 2012) and thus such a free choice is unlikely. For territorial birds, this Fretwell-Lucas model would predict a distribution in which the fittest males preferentially occupy the best sites and poorer sites are occupied by less competitive individuals, resulting in site-dependent breeding success (Sergio et al. 2007). Additionally, a pattern of sequential settlement according to individual quality and habitat quality (in our case morph type in accordance with habitat type) might only emerge over time. Thus, within our system, which involves a newly colonized population of a long-lived species with strong mate and site fidelity (Martin et al. 2014a), there may have been insufficient time to see such patterns emerge. However, the lack of spatial structuring may also be due to the fact that neither morph appeared to have an advantage within the more urbanized areas in terms of breeding performance, with no interaction found between morph and urbanization for any of the breeding parameters (productivity, breeding success, and brood size). Given that there was no significant difference in distribution of male or female morphs along the urban gradient, these results are not surprising.

Although we found no influence of urbanization on morph breeding performance, we did find that dark-morph males breed earlier in the year than light morphs, a result that had been found previously in this study population with a smaller sample size (Tate et al. 2016a). An earlier onset of breeding in dark-morph males is thought to be related to winter rainfall patterns (Martin et al. 2014b). The advantage for dark morphs breeding earlier in the year might be related to their higher prey provisioning rates in darker daylight hours (Tate et al. 2016b), that occur more frequently during the rainy season. Additionally, an earlier lay month in dark-morph males is known to have long-

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term fitness advantages for their offspring, which showed higher recruitment rates (Sumasgutner et al. 2016c).

Furthermore, the lack of relationship among breeding performance, morph, and urbanization might be related to prey abundance. Although we found differences in when (Tate et al. 2016b) and where (Tate and Amar in press) the different morphs hunted, there were no differences in the amount of food delivered to the nest (Tate et al. 2016b). No variation of main prey abundance was seen along the urban gradient in a previous study (Suri et al. 2017). Thus, food does not seem to structure the distribution of morphs, and is not a limiting factor in this urban Black Sparrowhawk population.

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AUTHOR CONTRIBUTIONS

The original idea and study design came from PS and AA. AK performed most of the fieldwork; help by others is accordingly acknowledged. SR and PS analyzed the data. The manuscript was prepared by PS, SR and AA.

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Appendix. LMMs and GLMMs investigating the relationship between the interaction of morph and urbanization with lay month, productivity, breeding success, and brood size. Separate analyses were conducted for male and female birds and their pair combination. The symbol × indicates an interaction term.

MODEL	RESPONSE	EXPLANATORY VARIABLES	ERROR STRUCTURE	*n*	df	ESTIMATE	SE	χ^2	*P*	SIGNIFICANCE[a]
Males	Lay month		Gaussian	426						
		urban gradient				−0.077	0.076	1.653	0.199	
		morph				0.384	0.134	8.138	0.004	***
		urban gradient × morph				−0.102	0.137	0.551	0.458	
		(intercept)				−0.071	0.084			
	Productivity		Negative binomial	426	417					
		lay month				−0.172	0.047	13.117	<0.001	***
		urban gradient				−0.006	0.057	0.093	0.760	
		morph				0.088	0.119	0.509	0.476	
		urban gradient × morph				−0.062	0.131	0.227	0.634	
		(intercept)				0.187	0.064		0.003	***
	Breeding success		Binomial	426	418					
		lay month				−0.673	0.160	17.705	<0.001	***
		urban gradient				−0.123	0.187	1.278	0.258	
		morph				0.660	0.417	2.063	0.151	
		urban gradient × morph				−0.518	0.413	1.575	0.210	
		(intercept)				1.048	0.213		<0.001	***

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Appendix. Continued.

Model	Response	Explanatory Variables	Error Structure	n	df	Estimate	SE	χ^2	P	Significance[a]
	Brood size		Poisson	301	293					
		lay month				−0.013	0.044	0.092	0.762	
		urban gradient				0.017	0.047	0.367	0.544	
		morph				−0.050	0.107	0.166	0.684	
		urban gradient × morph				0.061	0.118	0.267	0.605	
		(intercept)				0.614	0.048		<0.001	***
Females	Lay month		Gaussian	445						
		urban gradient				−0.075	0.086	1.542	0.214	
		morph				−0.089	0.126	0.475	0.490	
		urban gradient × morph				−0.041	0.126	0.104	0.747	
		(intercept)				0.032	0.086			
	Productivity		Negative binomial	445	436					
		lay month				−0.168	0.046	13.450	<0.001	***
		urban gradient				−0.040	0.063	0.070	0.792	
		morph				0.110	0.103	1.142	0.285	
		urban gradient × morph				0.068	0.099	0.473	0.491	
		(intercept)				0.177	0.064		0.006	**
	Breeding success		Binomial	445	437					
		lay month				−0.610	0.152	16.164	<0.001	***
		urban gradient				−0.388	0.212	1.148	0.284	
		morph				0.554	0.357	1.947	0.163	
		urban gradient × morph				0.582	0.349	2.782	0.095	•
		(intercept)				1.021	0.213		<0.001	***
	Brood size		Poisson	315	307					
		lay month				−0.023	0.042	0.292	0.589	
		urban gradient				0.050	0.055	0.398	0.528	
		morph				−0.021	0.090	0.061	0.805	
		urban gradient × morph				−0.056	0.084	0.442	0.506	
		(intercept)				0.613	0.050		<0.001	***
Pairs	Lay month		Gaussian	421						
		urban gradient						1.512	0.219	
		morph combination						10.342	0.016	*
		urban gradient × morph combination						2.262	0.520	
		(intercept)				−0.035	0.096			
	Productivity		Negative binomial	421	409					
		lay month						14.170	<0.001	***
		urban gradient						0.129	0.720	
		morph combination						2.402	0.493	
		urban gradient × morph combination						0.744	0.863	
		(intercept)				0.147	0.074		0.047	*

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Appendix. Continued.

MODEL	RESPONSE	EXPLANATORY VARIABLES	ERROR STRUCTURE	n	df	ESTIMATE	SE	χ^2	P	SIGNIFICANCE[a]
	Breeding success		Binomial	421	409					
		lay month						18.282	<0.001	***
		urban gradient						1.121	0.290	
		morph combination						3.723	0.293	
		urban gradient × morph combination						3.943	0.268	
		(intercept)				0.904	0.230		<0.001	***
	Brood size		Poisson	298	286					
		lay month						0.109	0.741	
		urban gradient						0.270	0.603	
		morph combination						1.278	0.734	
		urban gradient × morph combination						1.113	0.774	
		(intercept)				0.605	0.060		<0.001	***

[a] Significance codes: *** indicates $P < 0.001$; ** indicates $P < 0.01$; * indicates $P < 0.05$; • indicates $P > 0.10$.

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