ABSTRACT

Capsule: Urban Black Sparrowhawk males hunt mostly within 2.27 km of their nest during the breeding season (‘home range’ of 16.15 km²) and increased the distance slightly to 2.43 km outside of the breeding season (18.56 km²). We found high individual variation within and between six global positioning systems tagged breeding males, but no significant seasonal differences in the urban environment of Cape Town, South Africa.

Knowledge on the home range size of animals is vital to identify the appropriate scale at which to explore ecological relationships. Typically, the home range is the area in which an individual lives and moves in a defined time period and is related to the concept of an animal’s (smaller) territory that is actively defended (Burt 1943). Home range size may be estimated by means of a 95% kernel density (Worton 1989, Kenward et al. 2001a), synonymous to the utilization distribution (UD), which examines where the individual is likely to be for a given proportion of time. Estimates of these areas can play a vital role in helping to understand a species’ ecology, for example to explore how habitat may influence the ecology or breeding performance of a species, we require knowledge on the appropriate scale at which to test any relationships (Tanferna et al. 2013). Recent advances in tracking technology such as tracking devices using global positioning systems (GPS) have allowed accurate information on the ranging behaviour of bird species to be estimated with a high degree of accuracy. This information can help shape conservation strategies for threatened birds (Arroyo et al. 2014, Krüger et al. 2014, Reid et al. 2015), or can ensure assessment of the effect of environmental variables is conducted at the appropriate resolution and scale (Krüger et al. 2015, Sumasgutner et al. 2016).

Home range sizes may not be constant across time and may vary between seasons or between different stages of the breeding cycle. For example, species may show pronounced differences in the home range size between the breeding and non-breeding seasons (Krüger et al. 2014), between active breeders and floaters (Tanferna et al. 2013) or might be highly variable over the year (Village 1982). To disentangle seasonal home range sizes one requires data sets spanning the entire breeding period, ideally over several years, which are often not available in long-lived species such as raptors (Peery 2000, but see López-López et al. 2014 and Vasilakis et al. 2016 on vultures).

Urban ecology is one of the fastest growing fields in ecology (Shanahan et al. 2014, Beninde et al. 2015) and the need to understand how species cope and exploit urban environments is of growing importance as urban space increases globally together with the proportion of people living within urban environments (Ramalho & Hobbs 2012). Cities in Africa and Asia are urbanizing faster than any other regions in the world (United-Nations-Secretariat 2015), but specifically in these areas hardly any research is conducted to understand the impact of anthropogenic development on wildlife. Due to the loss of natural habitat, urbanization generally leads to a complete restructuring of vegetation and species composition and has become a major concern in conservation biology (Miller & Hobbs 2002).

Raptors vary in their adaptability to urbanization (Berry et al. 1998, Schmidt & Bock 2005) and individuals living in urban environments often differ from conspecifics living in rural habitats in their home range size and habitat use, but also in productivity (e.g. Sumasgutner et al. 2014) and survival (e.g. Altwegg et al. 2013). The degree of urbanization may have a strong influence on species home range sizes, which may be smaller in urban environments compared to...
rural areas for raptors specialized in avian prey (Sodhi & Oliphant 1992, Parker 1996, Mannan & Boal 2000, Dykstra et al. 2001, Coleman et al. 2002, Rutz 2006, Morrison et al. 2016), that benefit from an accumulation of prey-sized birds in the city (Sorace & Gustin 2009). On the other hand, unlike passerines, raptors have the capacity to extend their home range sizes beyond urban boundaries (Tella et al. 1996, Riegert et al. 2007a, 2007b) and therefore do not need to meet all their ecological requirements within inner-city districts. They might need to enlarge their territories to exploit suitable hunting grounds which might be sparsely distributed within urban areas (reviewed by Chace & Walsh 2006, Donázar et al. 2016). While urban environments may provide sufficient resources for some raptors, differences in species’ responses to urbanization indicate that the life history and ecology of raptors living in urban environments are not well understood.

Relatively few studies have explored the home range size of Accipiter hawks (Marquiss & Newton 1982, Kenward et al. 2001b, Roth et al. 2008) and even fewer have explored these home ranges in an urban environment (e.g. Mannan & Boal 2000, Rutz 2006). In this study we use GPS tags to explore the home range size of six adult male Black Sparrowhawks Accipiter melanoleucus and identify potential differences in more urbanized areas compared to suburban environments in Cape Town, South Africa (Amar et al. 2013). Additionally, using home range estimates across multiple months we examine if the UD varies between the breeding or non-breeding season and between different stages of the breeding period (pre-laying, incubation and nestling period).

Methods

Adult male Black Sparrowhawks were trapped on active territories (for details, see Martin et al. 2014a) using a bal-chatri trap baited with live white pigeons Columba livia (Berger & Müller 1959). They were fitted with GPS loggers (13 g solar powered EP3.5 ‘Harrier’ loggers by ECOTONE, Sopot, Poland) using a backpack harness made of Teflon tape. All GPS loggers were set to record satellite fixes every 15 minutes on a daily cycle from 4 am to 9 pm over several months from September 2012 until October 2015. These recorded between 9388 and 23 125 fixes per male; details in online supplement Table 1. Fixes recorded on the loggers were downloaded in territories once a month using a portable base station and directional antenna. The transmitters used were within the recommended upper limit of 3% of body mass (Kenward 1987): male body mass 430–490 g (Kemp & Kirwan 2016) and GPS tag 13 g (2.65–3% of body weight).

Home ranges, the UD, were estimated by means of a 95% kernel density approach (Worton 1989, Kenward et al. 2001a). For all spatial analyses the GPS fixes were projected to the Universal Transverse Mercator (UTM) coordinate system (World Geodetic System 1984 UTM Zone 35S). We estimated the ‘total home range size’ over the entire tracking period, as well as units of monthly home range sizes (30 days) and home range sizes for different stages of the breeding cycle (March to October with a peak during the winter months; Martin et al. 2014b). These home range sizes were estimated for each individual in R using the package ‘adegbhabitatHR’ classes and methods for home range estimation (Calenge 2006) with the package ‘rgdal’ (Bivand et al. 2014) to process the spatial data. We defined the breeding season as 30 days prior to clutch initiation (via video monitoring of the nest that was available for at least one breeding season per male, see Katzenberger et al. 2015 for details; or via behavioural observations during systematic nest monitoring), the incubation period of 34–38 days (Tarboton 2001) and the nestling period of 37–50+ days (Ferguson-Lees & Christie 2001) or until the nest failed. Kernel density estimates (KDE) were derived by fitting contour lines (isopleths) based on the volume of the curve under the UD which defined home range polygons whose areas were then calculated. Fixed 95% (‘home range’ thereafter), 90%, 75% and 50% kernel density contours were calculated to estimate the majority of the home range areas (90% and 75%), and the core (intensive use) areas (50%) (Fieberg 2007). A bivariate normal distribution was assumed to generate the UD kernels. Consequently the smoothing parameter was computed with the ad hoc method. We also calculated the overall space use of each individual as the Minimum Convex Polygon (MCP) encompassing 100% of all GPS fixes obtained for that individual (i.e. the entire area in which the individual male was located via GPS fixes over the whole tracking period).

We used generalized linear models (GLMs) to statistically compare home range sizes (UD kernel, in km², response variable) between individual birds (n = 6 males) and between different degrees of urbanization (as a continuous covariate). The degree of urbanization was extracted from the 2013–2014 South African National Land-Cover map (http://bgis.sanbi.org/DEA_Landcover/project.asp). We intersected the home range polygon (95% KDE) of each male with the provided land cover layer and summarized the percentage covered by buildings and traffic areas as ‘urban’.

Generalized linear mixed models (GLMMs, Gaussian distribution with identity link function and
individual as a random factor) in the package ‘lme4’ (Bates et al. 2014) were then used to compare the home range sizes (response variable) between the different stages of the breeding period (explanatory variable; see supplement Figure 1 for range changes over time). Due to high nest failure, not all males contributed data to all defined breeding stages (sample size varies between six males during the incubation phase and three during the pre-laying period). We only used fixes for the different breeding stages if available for a minimum of 20 days to ensure a sufficient sample size. All statistical analyses were performed with the software R version 3.2.3 (2015-12-10, R Development Core Team 2015).

Results and discussion

The mean (±sd) home range across the entire tracking period for six adult males was UD = 18.24 ± 12.75 km² based on their 95% kernel density estimation (Figure 1; note the larger MCPs based on all GPS fixes of 99.86 ± 84.10 km², range 41.01–264.64 km²). There was considerable individual variation (GLM, $\chi^2 = 42.34$, $P < 0.001$) ranging from 3.81 km² (‘Zonnestraal’-male, see supplement Figure 2 for full tracking period, September 2012 to April 2015) to 36.47 km² (‘Tokai Picnic’-male) and high individual seasonal variation (Figure 2).

The mean (±sd) home range size in the pre-laying period (defined here as one month prior to egg-laying) was 7.75 ± 5.85 km² ($n = 3$ males). In this period in more detail, the pre-laying home range was smaller for two males than the total home range size over the entire tracking period (46.1% and 27.1%, respectively). But one male showed a larger UD during the pre-laying period (10.51 km² during 30 days of pre-laying versus 7.93 km²). This might suggest a lower energy demand in the month before clutch initiation or more probably also the need to defend the territory, at least for some individuals. Territory defence might be necessary, for example, against nest usurpation by Egyptian geese.

Figure 1. Space use (MCP based on all GPS fixes and ‘home range size’ as 95% kernel density estimation) of male Black Sparrowhawks Accipiter melanoleucus on the Cape Peninsula plotted on an aerial image of Cape Town, South Africa. Black triangles: occupied Black Sparrowhawk nests in 2013. Lines showing the MCP for six radio-tagged individuals, dark shaded areas indicating the 95% kernel density estimation (defined as ‘home range’ in this study) and colour scale used to present the 90%, 75% and 50% kernel density estimation.
Alopench aegyptiaca (Curtis et al. 2007, Sumasgutner et al. 2016a) which might be habitat specific (Mackey & Lindenmayer 2001, Sumasgutner et al. 2016a) or against conspecifics (Martin et al. 2014a). Another reason might be to guard females from extra-pair copulation (Safina 1984, Rosenfield et al. 2015). However, across all birds these differences between the pre-laying period and the total home range size (over the entire tracking period) were not significant (GLMM, $\chi^2 = 1.68$, $P = 0.19$), suggesting this was not a general pattern found amongst individuals. As energy demands increase to feed the incubating female and later on the chicks, home range sizes increased slightly to 13.12 ± 13.33 km$^2$ ($n = 6$ males) during the incubation period and to 14.18 ± 15.48 km$^2$ ($n = 4$ males) during the nestling phase, but these apparent increases are driven by very large home range sizes of just two individuals during these periods (male 3 during incubation (38.76 km$^2$) and male 1 during the nestling phase (36.34 km$^2$)). Moreover, none of these breeding stages were significantly different to the total home range sizes of the hunting male (GLMMs: incubation: $\chi^2 = 1.91$, $P = 0.17$; nestling: $\chi^2 = 0.19$, $P = 0.66$), nor were they significantly different when comparing home range sizes across the different breeding stages (GLMMs: incubation versus pre-lay: $\chi^2 = 0.82$, $P = 0.37$; nestling versus pre-lay: $\chi^2 = 0.70$, $P = 0.40$; incubation versus nestling: $\chi^2 = 0.01$, $P = 0.91$).

Overall, home range sizes were slightly smaller during the breeding season (16.15 ± 12.75 km$^2$) than during the non-breeding season (18.56 ± 12.96 km$^2$), but these differences were not statistically significant (GLMM, $\chi^2 = 0.95$, $P = 0.33$). One might expect breeding season home ranges to decrease with latitude because of a dramatic increase in primary productivity in the summer at northerly latitudes (Peery 2000). However, in more tropical areas this difference is likely to be less stark and it therefore may be not surprising that we found no pronounced differences between the breeding and non-breeding stages in our study system, especially given the long breeding season ranging from March to October (Martin et al. 2014b).

Figure 2. Fifth per cent, 75% and 90% kernel density and home range (95% KDE) estimates in km$^2$ over the entire tracking period of six male Black Sparrowhawks A. melanoleucus and home range sizes over the breeding cycle (pre-laying, incubation and nestling period) and the non-breeding season of the same individuals where available. Note the colour coding of males 1–6 matches the map in Figure 1.
density dependence in space and time, with potentially staggered laying enabling high overall breeding densities in our study population (mean ± sd nearest neighbour distance between active territories in the year 2013: 1113 ± 802 m). This result is consistent with field observations suggesting that birds may delay breeding when territories are located very close to each other. Although speculative at this stage, this idea is worthy of further research.

In comparison with other hawks using urban environments for breeding we report quite large home range sizes. For example Cooper’s hawks Accipiter cooperii in Arizona, USA (Mannan & Boal 2000), had mean (±sd) home ranges of 65.5 ± 40.7 ha (range 13.3–130.6 ha), and Rutz (2006) found that adult male Northern Goshawks Accipiter gentilis in Hamburg, Germany, had home ranges of 863 ha. Both studies were based on the average 100% MCPs and not on kernel density estimations, which tend to be smaller (Figure 1). There is a clear lack of knowledge on the movement patterns and home range sizes of Black Sparrowhawks, particularly in an urban environment. However, the degree of urbanization did not explain the pronounced differences in home range sizes between male Black Sparrowhawks, and also underlines the importance of long-term tracking periods and need for larger samples sizes due to high individual variation in UD.

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References

Altweeg, R., Jenkins, A. & Abadi, F. 2013. Nestboxes and immigration drive the growth of an urban Peregrine Falcon Falco peregrinus population. Ibis 156: 107–115.

Amar, A., Koeslag, A. & Curtis, O. 2013. Plumage polymorphism in a newly colonized Black Sparrowhawk population: classification, temporal stability and inheritance patterns. J. Zool. 289: 60–67.

Arroyo, B., Leckie, F., Amar, A., Mccluskie, A. & Redpath, S. 2014. Ranging behaviour of Hen Harriers breeding in special protection areas in Scotland. Bird Study 61: 48–55.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Beninde, J., Veith, M. & Hochkirch, A. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18: 581–592.

Berger, D.D. & Müller, H.C. 1959. The bal-chatri: a trap for the birds of prey. Bird-Banding 30: 18–26.

Berry, M.E., Bock, C.E. & Haire, S.L. 1998. Abundance of diurnal raptors on open space grasslands in an urbanized landscape. The Condor 100: 601–608.

Bivand, R., Keitt, T. & Rowlingson, B. 2014. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.9-1.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346–352.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197: 516–519.

Chace, J.F. & Walsh, J.J. 2006. Urban effects on native avifauna: A review. Landsc. Urban Plann. 74: 46–69.

Coleman, J.L., Bird, D.M. & Jacobs, E.A. 2002. Habitat use and productivity of sharp-shinned hawks nesting in an urban area. The Wilson Bulletin 114: 467–473.

Curtis, O., Hockey, P. & Koeslag, A. 2007. Competition with Egyptian geese Alopecoen aegyptiaca overrides environmental factors in determining productivity of Black Sparrowhawks Accipiter melanoleucus. Ibis 149: 502–508.

Donázar, J.A., Cortés-Avizanda, A., Fargallo, J.A., Margalida, A., Moleón, M., Morales-Reyes, Z., Moreno-Opo, R., Pérez-García, J.M., Sánchez-Zapata, J.A., Züberogotita, I. & Serrano, D. 2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. Ardeola 63: 181–234.

Dykstra, C.R., Hays, J.L., Daniel, F.B. & Simon, M.M. 2001. Home range and habitat use of suburban red-shouldered hawks in southwestern Ohio. The Wilson Bulletin 113: 308–316.

Ferguson-Lees, J. & Christie, D.A. 2001. Raptors of the World. Houghton Mifflin, Boston, MA.

Fieberg, J. 2007. Kernel density estimators of home-range: smoothing and the autocorrelation of herring. Ecology 88: 1059–1066.

Katzenberger, J., Tate, G., Koeslag, A. & Amar, A. 2015. Black Sparrowhawk brooding behaviour in relation to chick age and weather variation in the recently colonized Cape Peninsula, South Africa. J. Ornithol. 156: 903–913.

Kemp, A.C. & Kirwan, G.M. 2016. Black Sparrowhawk (Accipiter melanoleucus). In Del Hoyo, J, Elliott A, Sargatal, J, Christie, D.A. & De Juana, E. (eds) Handbook of the Birds of the World Alive, Lynx Edicions, Barcelona.

Kenward, R. 1987. Wildlife Radio Tagging. Academic Press, London.
Kenward, R.E., Clarke, R.T., Hodder, K.H. & Walls, S.S. 2001a. Density and linkage estimators of home-range: nearest-neighbor clustering defines multi-nuclear cores. *Ecology* 82: 1905–1920.

Kenward, R.E., Clarke, R.T., Hodder, K.H. & Walls, S.S. 2001b. Density and linkage estimators of home range: Nearest-neighbor clustering defines multinuclear cores. *Ecology* 82: 1905–1920.

Krüger, S., Reid, T. & Amar, A. 2014. Differential range use between age classes of Southern African bearded vultures *Gypaetus barbatus*. *PLoS ONE* 9: e114920.

Krüger, S.C., Simmons, R.E. & Amar, A. 2015. Anthropogenic activities influence the abandonment of bearded vulture (*Gypaetus barbatus*) territories in southern Africa. *Condor* 117: 94–107.

López-López, P., García-Ripollés, C. & Urios, V. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecol. Appl.* 24: 938–949.

Mackey, B.G. & Lindenmayer, D.B. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. *J. Biogeogr.* 28: 1147–1166.

Mannan, R.W. & Boal, C.W. 2000. Home range characteristics of male Cooper’s Hawks in an urban environment. *Wilson Bull.* 112: 21–27.

Marquiss, M. & Newton, I. 1982. A radio-tracking study of the ranging behaviour and dispersion of European Sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* 51: 111–133.

Martin, R.O., Koeslag, A., Curtis, O. & Amar, A. 2014a. Fidelity at the frontier: divorce and dispersal in a newly colonized raptor population. *Anim. Behav.* 93: 59–68.

Martin, R.O., Sebele, L., Koeslag, A., Curtis, O., Abadi, F. & Amar, A. 2014b. Phenological shifts assist colonisation of a novel environment in a range-expanding raptor. *Oikos* 123: 1457–1468.

Miller, J.R. & Hobbs, R.J. 2002. Conservation where people live and work. *Conserv. Biol.* 16: 330–337.

Morrison, J.L., Gottlieb, I.G.W. & Pias, K.E. 2016. Spatial distribution and the value of green spaces for urban red-tailed hawks. *Urban Ecosyst.* doi:10.1007/s11252-016-0554-0.

Parker, J.W. 1996. Urban ecology of the Mississippi Kite. In Bird, D.M. Varland, D.E. & Negro, J.J. (eds) *Raptors in Human Landscapes: Adaptations to Built and Cultivated Environments*, 45–52. Academic Press, London.

Peery, M.Z. 2000. Factors affecting interspecies variation in home-range size of raptors. *The Auk* 117: 511–517.

Ramalho, C.E. & Hobbs, R.J. 2012. Time for a change: dynamic urban ecology. *Trends Ecol. Evol.* 27: 179–188.

Reid, T., Krüger, S., Whitfield, D.P. & Amar, A. 2015. Using spatial analyses of bearded vulture movements in southern Africa to inform wind turbine placement. *J. Appl. Ecol.* 52: 881–892.

R Development Core Team 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Riegert, J., Dušek, A., Fainová, D., Mikes, V. & Fuchs, R. 2007a. Increased hunting effort buffers against vole scarcity in an urban Kestrel *Falco tinnunculus* population. *Bird Study* 54: 353–361.

Riegert, J., Fainová, D., Mikes, V. & Fuchs, R. 2007b. How urban Kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation? *Acta Ornithol.* 42: 69–76.

Rosenfield, R.N., Sonsthagen, S.A., Stout, W.E. & Talbot, S.L. 2015. High frequency of extra-pair paternity in an urban population of Cooper’s Hawks. *J. Field Ornithol.* 86: 144–152.

Roth, T.C., Vetter, W.E. & Lima, S.L. 2008. Spatial ecology of wintering *Accipiter* Hawks: home range, habitat use, and the influence of bird feeders. *The Condor* 110: 260–268.

Rutz, C. 2006. Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *Ardea* 94: 185–202.

Safina, C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. *Oikos* 43: 159–164.

Schmidt, E. & Bock, E.C. 2005. Habitat associations and population trends of two hawks in an urbanizing grassland region in Colorado. *Landsc. Ecol.* 20: 469–478.

Shanahan, D.F., Strohbach, M.W., Warren, P.S. & Fuller, R.A. 2014. The challenges of urban living. In Gil, D. & Brumm, H. (eds) *Avian Urban Ecology. Behavioural and Physiological Adaptations*, 3–20. Oxford University Press, Oxford.

Sodhi, N.S. & Oliphant, L.W. 1992. Hunting ranges and habitat use and selection of urban-breeding merlins. *The Condor* 94: 743–749.

Sorace, A. & Gustin, M. 2009. Distribution of generalist and specialist predators along urban gradients. *Landsc. Urban Plan.* 90: 111–118.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H.W. & Gamauf, A. 2014. Hard times in the city – attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Frontiers in Zoology* 11: 48.

Sumasgutner, P., Millán, J., Curtis, O., Koelsag, A. & Amar, A. 2016a. Is multiple nest building an adequate strategy to cope with inter-species nest usurpation? *BMC Evol. Biol.* 16: 97.

Sumasgutner, P., Tate, G.J., Koeslag, A. & Amar, A. 2016b. Family morph matters: factors determining survival and recruitment in a long-lived polymorphic raptor. *J. Anim. Ecol.* 85: 1043–1055.

Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F. & Sergio, F. 2013. Habitat selection by Black kite breeders and floaters: implications for conservation management of raptor floaters. *Biol. Conserv.* 160: 1–9.

Tarboton, W.R. 2001. Guide to the Nests and Eggs of Southern African Birds. Struik Publishers, Cape Town.

Tella, J.L., Hiraldo, F., Donazar-Sancho, J.A. & Negro, J.J. 1996. Costs and benefits of urban nesting in the Lesser Kestrel. In Bird, D.M. Varland, D.E. & Negro, J.J. (eds) *Raptors in Human Landscapes, Adaptations to Built and Cultivated Environments*, 3–60. Academic Press, New York.

United-Nations-Secretariat. 2015. *World Urbanization Prospects: The 2014 Revision*. Department of Economic and Social Affairs, United Nations, New York.

Vasilakis, D.P., Whitfield, D.P., Schindler, S., Poirazidis, K.S. & Kati, V. 2016. Reconciling endangered species conservation with wind farm development: Cinereous vultures (*Aegypius monachus*) in south-eastern Europe. *Biol. Conserv.* 196: 10–17.

Village, A. 1982. The home range and density of kestrels in relation to vole abundance. *J. Anim. Ecol.* 51: 413–428.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.