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Authors: van Velden, Julia L., Koeslag, Ann, Curtis, Odette, Gous, Tertius, and Amar, Arjun

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RESEARCH ARTICLE

Negative effect of mite (*Knemidokoptes*) infection on reproductive output in an African raptor

Julia L. van Velden,^{1*} Ann Koeslag,¹ Odette Curtis,² Tertius Gous,³ and Arjun Amar¹

¹ FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

² Overberg Lowlands Conservation Trust, Napier, South Africa

³ Helderberg, South Africa

* Corresponding author: juliavanvelden@gmail.com

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ABSTRACT

Knemidokoptes is a genus of subcutaneous mites found in the skin of multiple avian hosts, although few cases have been reported in wild raptors. Population monitoring of Black Sparrowhawks (*Accipiter melanoleucus*) on the Cape Peninsula, South Africa, between 2001 and 2012 revealed multiple birds with infection symptoms in some years. Examination of 3 dead birds displaying symptoms such as baldness and skin lesions confirmed infection by *Knemidokoptes* spp., whereas we found no cases of subclinical infection in birds without symptoms ($n = 16$). Up to 5% of birds in the population were infected in some years, which represents the first record of multiple birds displaying an infection by *Knemidokoptes* in a wild population of raptors. A male bias in infection prevalence was detected. Prevalence of infection symptoms was generally low in other populations elsewhere in South Africa, although possibly higher in urban areas. Breeding performance (both productivity and nesting success) was significantly lower for individuals following infection and also in comparison with noninfected birds throughout the study period. This is the first study to demonstrate the negative effect that these mites may have on breeding performance in a wild bird species, and our results suggest that this parasite could potentially influence population dynamics over time.

Keywords: Black Sparrowhawk, breeding performance, *Knemidokoptes*, nesting success, parasites, productivity

Effet négatif d'une acariase causée par *Knemidokoptes* sur l'efficacité de la reproduction d'un rapace africain

RÉSUMÉ

Les acariens du genre *Knemidokoptes* sont des acariens sous-cutanés que l'on trouve dans la peau de nombreux hôtes aviaires, bien que peu de cas aient été rapportés chez les rapaces sauvages. Le suivi des populations d'*Accipiter melanoleucus* dans la péninsule du Cap, en Afrique du Sud, entre 2001 et 2012, a révélé que de nombreux oiseaux présentaient des symptômes d'infection au cours de certaines années. L'examen de trois oiseaux morts présentant des symptômes tels que la calvitie et des lésions cutanées a révélé une acariase causée par *Knemidokoptes*, alors que nous n'avons trouvé aucun cas d'infection subclinique chez les oiseaux sans symptômes ($n=16$). Près de 5 % des oiseaux de la population étaient infectés lors de certaines années, ce qui représente la première mention de plusieurs oiseaux souffrant d'une acariase causée par *Knemidokoptes* dans une population sauvage de rapaces. Un biais en faveur des mâles dans la prévalence de l'infection a été détecté. La prévalence des symptômes d'infection était généralement faible dans les autres populations ailleurs en Afrique du Sud, bien que possiblement plus élevée dans les zones urbaines. La performance reproductive (productivité et succès de nidification) était significativement plus faible chez les individus après l'infection et comparativement aux oiseaux non infectés tout au long de la période étudiée. Il s'agit de la première étude démontrant l'effet négatif que ces acariens peuvent avoir sur la performance reproductive d'une espèce d'oiseau sauvage; elle suggère que ce parasite peut potentiellement influencer la dynamique des populations dans le temps.

Mots-clés: *Accipiter melanoleucus*, performance reproductive, *Knemidokoptes*, succès de nidification, parasites, productivité

INTRODUCTION

How parasites and their hosts interact has fascinated biologists for centuries (Darwin 1859). Bird–parasite interactions have proved particularly useful in demon-

strating how parasites can mediate the ecology and evolution of their hosts (Proctor and Owens 2000). Research suggests that parasites can be as important as predators or resource limitation in limiting the growth of host populations (Anderson and May 1979). This contrasts

with the alternative paradigm of “successful” parasites evolving to do little or no harm to their hosts, with commensalism as the end result of the interaction between host and parasite (Toft 1991). There is, however, considerable evidence against this theory, with many cases showing that parasites may negatively affect reproduction (Møller 1993, Richner et al. 1993, Fitze et al. 2004) and survival (Richner and Tripet 1999), which, in turn, can influence the host species’ population dynamics and evolution (Toft 1991).

Parasite loads are rarely distributed evenly within populations (Clayton and Moore 1997), and parasite prevalence or intensity may vary across ages, sexes, or color morphs (Christe et al. 2007, Lei et al. 2013). In many cases, males may show greater prevalence and intensity of parasites than females as a result of fundamental biological and behavioral differences (Christe et al. 2007), and such male biases are seen in both birds and mammals (Poulin 1996). These differences may be due to steroid hormones such as testosterone, which, while enhancing the male host’s secondary sexual characteristics, can also suppress its immune system (Folstad and Karter 1992). Behavioral differences such as aggression between males or decreased male grooming during the mating season may also account for this bias (Christe et al. 2007). Furthermore, age can also be significant in determining parasite levels. Older individuals can have significantly higher parasite burdens, possibly due to differences in hormonal exposure (Weatherhead and Bennet 1991, Norris et al. 1994, Deviche et al. 2001) or simply due to their length of exposure to potential parasites or vectors. Alternatively, younger individuals may have higher parasite burdens because they have yet to acquire immunity or resistance (Lei et al. 2013).

Parasitic mites are a taxonomically diverse group, including $\geq 2,500$ species that are dependent on birds (Proctor and Owens 2000). Mites and their avian hosts have highly diverse relationships, ranging from detrimental to beneficial for their hosts. The genus *Knemidokoptes* (Acari: Knemidokoptidae) is a relatively understudied group of subcutaneous mites found in the skin of the face, legs, or body of avian hosts. They feed on the host’s tissue or eat the feather quill’s pith (Proctor and Owens 2000, Dabert et al. 2013), and infection can result in the condition known as “scaly leg,” “scaly face” (Kirmse 1966), or “depluming itch.” Symptoms of infection include feather loss, lesions on the face and beak, and lesions and encrustations on legs or body (Pence 2008). Proliferation of growths can cause beak deformities and loss of digits (Pence 2008, Goulding et al. 2012). About 20 wild passerines from a variety of families are known hosts (Latta and O’Connor 2001). The propensity of these mites to cause epizootic events has been documented in poultry, in caged birds, and, increasingly, in wild birds (Pence et al. 1999).

In one of the very few studies that have explored the fitness consequences in wild birds of infection by *Knemidokoptes*, Latta (2003) examined infections in Prairie Warblers (*Setophaga discolor*) and Palm Warblers (*S. palmarum*) in the Dominican Republic. He found that mite infection caused significantly reduced muscle-mass scores, reduced site persistence, and reduced annual return rates after migration—factors that are indicative of lower survival rates. The compromised physiological condition of the parasitized individual may increase susceptibility to mortality during migration, even when the mite infection may not be fatal in itself (Latta 2003). This study and a previous one (Latta and O’Connor 2001) both found that habitat was an important variable, that *Knemidokoptes* infections were more common in dry desert scrub than at higher elevations and in moist habitats, and that there was a positive relationship between dry habitat type and the prevalence of infections. A dry environment like that of the desert thorn scrub could exert greater physiological stress than moist habitats, which could promote transmission to a weakened bird. Suboptimal habitats may necessitate increased expenses of time and energy in foraging, a cost that may suppress the bird’s immune function. Alternatively, dry desert habitats may be conducive to a favorable mite microclimate, aiding the latter’s survival and reproduction (Latta 2003).

Knemidokoptes infestations appear to be uncommon in birds of prey (Miller et al. 2004). The 3 recorded cases were all in captive individuals: a Swainson’s Hawk (*Buteo swainsoni*; Miller et al. 2004), a captive Great Horned Owl (*Bubo virginianus*; Schulz et al. 1989), and a captive hybrid falcon (*Falco* spp.; Heidenreich 1997). In the only study conducted on *Knemidokoptes* in Africa, focused on the Cape Wagtail (*Motacilla capensis*) population of Dassen Island, Goulding et al. (2012) found that infection by *Knemidokoptes jamaicensis* was more than twice as prevalent on this island as on the mainland, perhaps due to lower predation rates on the island. Goulding et al. (2012) also found that larger individuals were more likely to exhibit signs of infection.

Black Sparrowhawks (*Accipiter melanoleucus*) have recently colonized the Cape Peninsula, South Africa, the first successful breeding attempt having been recorded in 1993 (Oetlé 1994). Since then, the population has increased substantially to an estimated 50 breeding pairs (Martin et al. 2014a). Despite this apparent success, a number of birds with balding heads and/or leg lesions have been seen in this population in recent years. These symptoms were considered to indicate infection by *Knemidokoptes*, and a postmortem on a dead bird found with these symptoms appeared to confirm this, the death being attributed to a severe mite infestation (MacGregor 2012). No abnormalities were detected in the organs of this

bird, apart from severe mite infection, pectoral muscle atrophy, and reduced fat reserves.

In the present study, we investigated infection of Black Sparrowhawks by this parasite in more detail and examined the influence that infection might have on an individual's reproduction. First, we tested whether the symptoms described above were indeed closely associated with *Knemidokoptes* infection by examining the latter's presence in 19 dead birds, 3 of which showed visual symptoms; the other 16 were asymptomatic and thus could be used to explore subclinical prevalence. If symptomatic birds were positive for mites and asymptomatic birds were not, this would indicate that visual observation can be used to accurately monitor the prevalence of this parasite in a population. Second, we determined the frequency of occurrence of these symptoms on the Cape Peninsula over a 12 yr period (2001–2012) and examined whether the occurrence of these symptoms differed between sexes or between morphs of this polymorphic species (Amar et al. 2013). Third, using historical data, we examined the extent of the occurrence of these symptoms elsewhere across South Africa. Finally, to examine whether mite infection influenced the reproductive output of infected birds within the Cape Peninsula, we (1) explored nesting success (either successful, with chicks fledged; or unsuccessful, where the nest failed at any stage between courtship and fledging) and productivity (the number of chicks produced) before and after infection for individually identifiable birds; and (2) compared breeding attempts across the population for pairs containing either infected or noninfected birds.

METHODS

Monitoring of the Cape Peninsula Population

We used data from the monitored Black Sparrowhawk population on the Cape Peninsula from 2001 to 2012. The study area featured a matrix of habitats, including urban gardens, alien pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.) plantations, and small pockets of indigenous Afri-montane forest and Fynbos (Curtis et al. 2007). Our study area covered a surface of approximately 35×17 km². For a map of the study area and locations of nests, see Martin et al. (2014a). Altitudes where the birds breed range from sea level to ~300 m, and the climate is temperate, with locally variable winter rainfall (Martin et al. 2014a).

Monitoring was conducted during the breeding season (March–November) in each year (Martin et al. 2014a, 2014b). Territories were visited regularly (approximately monthly) throughout the season until breeding was detected, and then breeding attempts were monitored weekly until conclusion. Where possible, we identified the sex-specific morphs (dark or light) of both parents

attending a nest, which was possible in ~90% of breeding attempts. The species is easy to sex visually, males weighing ~60% less than females (Ferguson-Lees and Christie 2001). We fitted unique color-ring combinations to as many breeding adult birds and nestlings (2–3 wk old) as possible. Adults were trapped on territories using a bal-chatri trap baited with live white Domestic Pigeons (*Columba livia domestica*; Berger and Mueller 1959). During breeding monitoring, we recorded the color-ring combination of any ringed birds. During observation with binoculars or a digital camera, we recorded the occurrence of any individual Black Sparrowhawk showing visual symptoms of *Knemidokoptes* infection. Sightings of nonbreeding birds with visual symptoms were also recorded and occurred primarily at monitored breeding territories, but sporadic observations outside of breeding territories, such as photographs taken by the public, were also used. The use of visual observations may cause a bias toward heavily infected birds with obvious symptoms. These results are therefore likely to be an underestimate of the true prevalence of infection.

Sampling Dead Birds for Mite Infection

The presence of *Knemidokoptes* infections was investigated on 19 deceased Black Sparrowhawks, which had been found dead from various causes such as road accidents or collisions with windows. We aimed to confirm whether symptomatic birds were indeed infected by *Knemidokoptes*, as suspected, and also whether any nonsymptomatic birds showed subclinical effects. Corpses were frozen and skin scrapings taken from a random leg and from the head of the bird using anatomical markers—namely, from the halfway point of the tarsometatarsus, at both the front and the back of the leg; from the top or side of each toe; and from the crown of the bird's head. A total of 7 skin samples were taken from each bird. The scrapings were taken from just under the leg scales or feathers of the bird, using a scalpel, and placed on individual slides. A small amount of potassium hydroxide (10% KOH) was added to each scraping, in order to macerate the waxy layer of the scales and skin (Schulz et al. 1989, Pence et al. 1999). A coverslip was applied and the slides were examined at 40× magnification with a compound microscope. The presence of mites was noted for each slide. All slides received the same search effort of ~5 min per slide, in order to standardize effort and ensure efficient and thorough examination. Additionally, a heavily symptomatic male bird (specimen A) was sent for postmortem examination by the Western Cape state veterinarian (MacGregor 2012).

Establishing Infections Elsewhere in South Africa

We contacted researchers elsewhere in South Africa who had monitored Black Sparrowhawks to establish whether they had seen birds with symptoms of *Knemidokoptes*

TABLE 1. Information on symptoms of mite infection in Black Sparrowhawks across South Africa, including the source, time period, location, and number of breeding events (*n*) for each study.

Source	Period	Location	<i>n</i>
Tarboton and Allan 1984	1976–1980	Nylsvley	118
E. Wreford personal communication	2011–2012	Kwa-Zulu Natal	29
Malan and Robinson 2001	2001	Across South Africa	58
H. Chittenden personal communication	2010–2011	Kwa-Zulu Natal	2
http://fireflyafrica.blogspot.com/2012/07/black-sparrowhawk.html	2012	Port Elizabeth	1
Present study	2001–2012	Cape Peninsula	442
Tate et al. 2016	2014	Across South Africa	109
Total			759

infection (i.e. baldness and leg lesions). Sources of this information are summarized in Table 1. For sites or studies with multiple monitored pairs, we also obtained information on the number of breeding events monitored and the number of infected birds seen. The percentage of the breeding population that was infected was calculated and compared with that of the Cape Peninsula population.

Statistical Analysis

We used a chi-square test to examine whether either sex or morph (dark or light) was infected at a higher rate than expected. This analysis used the data on prevalence of infection symptoms in wild, live, infected individuals ($n = 20$). Expected proportions of infected individuals of the 2 morphs, based on the average percentages of dark and light birds in the population (i.e. 76% dark and 24% light; Amar et al. 2013), were applied to all infected individuals of known morph ($n = 20$). We estimated the expected numbers of infected males and females from all observed infected individuals of known sex ($n = 14$), assuming a balanced 1:1 sex ratio (Brown and Brown 1979).

To explore the influence of infection on nesting success and productivity, 2 separate analyses were performed using generalized linear mixed models (GLMM) in R (R Development Core Team 2013). Our first analysis assessed the difference in breeding performance before and after infection, at the level of the individual, using birds that were individually recognizable between years. We also analyzed the relationship of infection to nesting success and to productivity. Nesting success was treated as binomial (1 = successful breeding, 0 = unsuccessful breeding), where unsuccessful breeding occurred if the nest failed at any stage between courtship and the chicks leaving the nest. Productivity, defined as the number of chicks surviving to leave the nest for any breeding event, ranged from 0 to 3 chicks and approximated a Poisson distribution.

Each bird in the first analysis was given a unique identifier, which was specified as a random term to control for the nonindependence of samples for the same bird prior to and after infection. Even when an infected bird was unringed, it could be reliably identified by its morph,

its sex, and the presence of infection, and therefore breeding outcome could still be determined and attributed to specific birds. Individuals could be identified relatively accurately because this was a small population in which pairs and individuals were relatively faithful to nesting territories (Martin et al. 2014a). If a bird was not color ringed, the combination of its lack of color rings (>75% of adults were color ringed), its infection status, and its morph could be used to reliably identify the individual.

Our second analysis explored the breeding performance of a pair within a year, in relation to whether the pair contained an infected bird or not. This analysis therefore took advantage of our more extensive dataset. We included only years in which at least one individual of a pair was infected (2007–2012). The effects of infection on both nesting success and productivity were analyzed. We included “year” and “territory” as random variables within this GLMM. Although the variable “territory” was used in this analysis, in the majority of cases this equates to a unique identifier of a “pair.” The analysis therefore examined the reproductive output of a pair breeding at a territory in relation to the infection status of the pair, and also compared pairs within the same year. Preliminary analyses using a general linear model (with age fitted as the response variable and sex fitted as an explanatory variable) confirmed that there was no difference in mean age between infected and uninfected birds (females: infected mean age = 6.38 yr, uninfected mean age = 5.77, $F = 0.586$, $df = 191$, $P = 0.444$; males: infected mean age = 6.90, uninfected = 5.81, $F = 1.499$, $df = 170$, $P = 0.22$).

RESULTS

Confirmation of *Knemidokoptes* Infection

Among the 19 dead individuals sampled using skin scrapings, 3 adult males were found to be infected with *Knemidokoptes*. Two individuals had severe symptoms (specimen A: bald with severe leg lesions; specimen B: bald with “scaly” legs but with no obvious leg lesions), and microscopic examination of skin scrapings confirmed that both were infected on the head and legs with *Knemidokoptes*. Specimen A was confirmed as infected through a



FIGURE 1. Female Black Sparrowhawk with symptoms of mite infection; note the bald head and severe leg lesions. Photo credit: G. Tate

postmortem carried out by the state veterinary laboratory, and specimen B was confirmed as infected using the same microscopic examination of skin scrapings by one of the authors (J.V.V.). One other individual (specimen C), which had only a very small lesion on the leg, was also found to be infected by *Knemidokoptes*; in this case, however, the symptoms would probably not have been detected from general visual observation of the free-living bird. The mites were identified as *Knemidokoptes* spp. by one of the authors (T.G.) and further confirmed by Heloise Heyne of Onderstepoort Veterinary Institute, although the species was not identified. Mites were seen in burrows they had excavated in the skin at a subcutaneous level.

None of the 16 Black Sparrowhawk carcasses without visual symptoms were found to be infected with mites (including 6 adult males, 4 adult females, 3 juvenile males, and 3 juvenile females). It therefore appears that the symptoms of bald head and leg lesions (Figure 1) were exclusively linked with infection by *Knemidokoptes* in this species of bird, and it also appears that there is little subclinical infection by this parasite. However, we cannot

infer subclinical prevalence conclusively with only 16 samples.

Temporal Prevalence of Infection within the Cape Peninsula Population

Between 2001 and the end of 2012, within the Cape Peninsula study area, we observed 20 cases of live birds with infection symptoms among a maximum of 98 ringed birds (20.4%). In total, 442 breeding events have been monitored in this population. Of the 20 infected birds, 10 were part of a breeding pair, whereas the other 10 birds were observed outside of territories and could not be ascribed to a pair. Multiple infections appeared to occur in the same years (Figure 2) and only started appearing once the population had exceeded 25 territorial pairs.

Among these 20 wild, live, infected birds, 13 were dark and 7 were light morphs. The ratio of infected birds of the 2 morphs did not differ significantly from expected given the proportion of dark and light birds in this population, in which dark morphs are more prevalent (76% dark morph; $\chi^2 = 1.33$, $P = 0.25$). Among the 14 infected birds of known sex were 11 males and 3 females; assuming a 1:1 sex ratio, the proportion of males infected was significantly higher than expected ($\chi^2 = 4.57$, $P = 0.03$).

Nesting Success and Productivity in Relation to Infection Status

To investigate the effect of infection on breeding performance, we carried out 2 separate analyses. Our first analysis examined breeding performance before or after infection for recognizable individuals. There were data on nesting success and productivity for 10 individuals, which spanned 34 breeding attempts, including 15 before infection and 19 during or after infection. We found that both nesting success (whether young fledged or not) and productivity (total number of chicks fledged) were significantly lower once a member of the pair was infected, compared to these values prior to infection (nesting success: $\chi^2 = 4.06$, $P = 0.044$; productivity: $\chi^2 = 5.560$, $P = 0.018$). The estimates of the coefficient were -0.32 (95% confidence interval [CI]: -0.64 to -0.01) for nesting success and -1.38 (95% CI: -2.52 to -0.23) for productivity. For those individuals that became infected (i.e. showed symptoms), average nesting success (\pm SE) was 0.53 ± 0.13 prior to infection but fell to 0.21 ± 0.09 following infection, and average productivity was 1.24 ± 0.31 prior to infection but fell to 0.29 ± 0.17 following infection (Figure 3).

Our second analysis included all breeding attempts by all birds in years in which at least one bird from a pair was infected (2007–2012) and compared breeding performance of pairs with at least one infected bird to that of uninfected pairs. Between 2007 and 2012, we recorded the outcomes of 247 breeding attempts, 18 of which had at

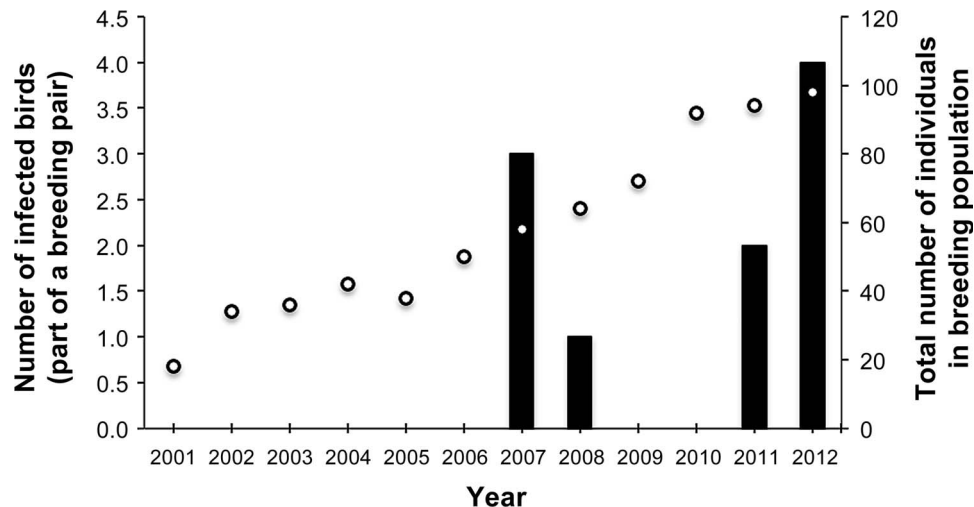


FIGURE 2. Number of infected Black Sparrowhawks (bars) that were part of a breeding pair in the Cape Peninsula population for each year of the study, compared to the total number of birds in the breeding population (points).

least one infected bird present. Five of the infected birds had multiple breeding attempts included in this analysis, while 6 birds had only a single breeding attempt included. The results were similar to those of our first analysis, with significantly lower productivity ($\chi^2 = 10.70$, $P = 0.001$) and nesting success ($\chi^2 = 12.12$, $P < 0.001$) for breeding attempts including infected birds. The estimates of the coefficient were -1.51 (95% CI: -2.40 to -0.60) for productivity and -2.54 (95% CI: -3.96 to -1.11) for nesting success. The values were similar to those in the previous analysis, with an average (\pm SE) nesting success of 0.66 ± 0.03 for noninfected pairs but only 0.16 ± 0.09 for pairs with at least one infected partner, and average productivity of 1.19 ± 0.08 for noninfected pairs but only 0.26 ± 0.15 for infected pairs. In 9 of 18 infection cases (50%), breeding failure could not be attributed to a specific cause other than mite infection itself; and in 5 of these 9 cases, breeding failed at the nest-building stage. Among the other 9 infection cases in which a cause of failure was known, there were 4 cases of failure due to geese harassment, 3 cases in which the female was suspected to be infertile, and 2 cases in which the nest tree was disturbed by humans.

Infections by *Knemidokoptes* Elsewhere in South Africa

Including the Cape Peninsula, only 5 areas of South Africa had reports of Black Sparrowhawks with symptoms of mite infection such as balding and leg lesions. Besides the Cape Peninsula, we obtained records of birds with infection symptoms in Port Elizabeth, Dullstroom, Nkaleni Valley, and around the Durban area (Figure 4). No infections were reported in the rest of the country. Port Elizabeth was found to have the highest number of infections in relation

to the number of breeding events studied (3/18), followed by Durban (3/50) and the Cape Peninsula (20/447). Infections around the Durban area were recorded only in recent years (2011 and 2012): E. Wreford recorded 3 infections from 29 breeding events (Table 1). Within the former Transvaal area (Nylsvley), Tarboton and Allan (1984) monitored 118 breeding events and recorded no cases of infection. Across South Africa, Malan and Robinson (2001) monitored 58 breeding events and recorded no incidence of infection. Finally, a wide survey across South Africa in 2014 by Tate et al. (2016) reported 3 birds with infections (2 in Port Elizabeth and 1 in Dullstroom). Thus, it appears that infection has only been

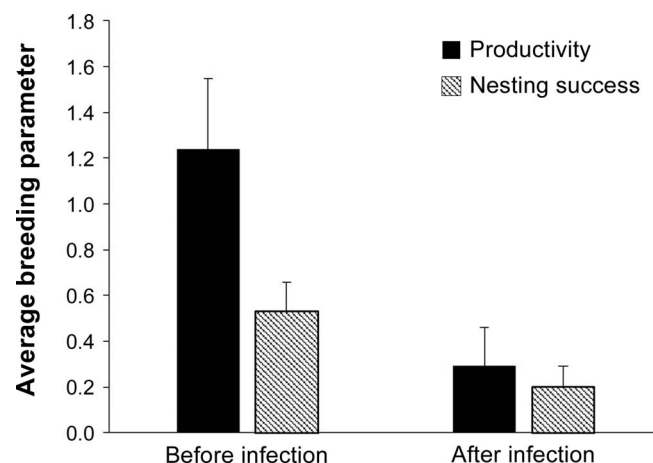


FIGURE 3. Average (\pm SE) nesting success (hatched bars) and productivity (black bars) of individual Black Sparrowhawks that were part of a breeding pair—recorded as infected ($n = 10$), before infection, and after infection—during breeding on the Cape Peninsula between 2001 and 2013. Differences before and after infection were significant ($P < 0.05$) for both variables.

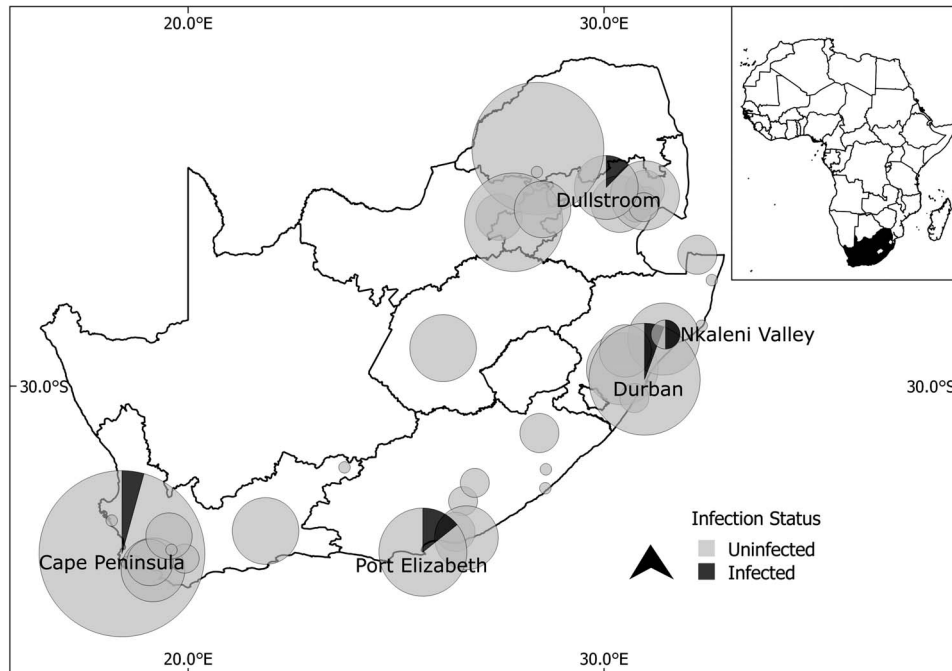


FIGURE 4. Map of South Africa showing the distribution of monitored Black Sparrowhawks. The size of each circle is proportional to the log number of breeding events monitored in the respective area. Gray portions of each pie chart represent the proportion of uninfected breeding events studied, and black the proportion of birds with symptoms of infection by mites in the genus *Knemidokoptes*.

witnessed over the past decade and is largely confined to urban areas.

DISCUSSION

We found evidence consistent with the assumption that the symptoms (bald heads and leg lesions) suspected of being the result of infection by *Knemidokoptes* were indeed associated exclusively with infection by this subcutaneous parasitic mite. Our study is the first to report a large number of clinical *Knemidokoptes* infections in a wild population of a bird of prey. Among the 16 Black Sparrowhawks that showed no such symptoms, none were found to be infected. These results suggest that observations of symptomatic birds can be used to monitor the prevalence of this parasite in a population and that subclinical levels of infection are low. The prevalence of subclinical infection by *Knemidokoptes* in other captive and wild birds is undocumented (Pence et al. 1999). We were unable to confirm the exact species of mite because genetic identification to the species level is currently limited by a lack of reference sequences.

Importantly, this is the first time that reduced breeding performance has been found in birds with *Knemidokoptes* infections, which was evident both when comparing breeding performance before and after severe infection and also from the larger analysis comparing breeding

performance of noninfected and infected pairs. Following infection, nesting success and productivity were at less than half the level found prior to infection. This is, however, a correlative study, and it cannot be said that mite infection definitely caused the reduction in breeding performance. A bird in an already weakened state could be more susceptible to infection, given that metabolic stress causes immunosuppression and, thus, increased susceptibility to parasitic diseases (Folstad and Karter 1992, Deerenberg et al. 1997), and this weakened state would negatively affect breeding separately. Interestingly, the productivity of infected birds before infection was similar to overall productivity levels for the uninfected population as a whole (i.e. 1.24 ± 0.31 for 35 breeding attempts vs. 1.19 ± 0.04 for 352 breeding attempts), and so infected birds were not necessarily those already in poorer condition or inhabiting lower-quality territories. If that had been the case, we might have expected to see lower productivity before infection compared to the productivity of other birds. This depressed nesting success and productivity of infected birds indicates that, in theory, this parasite has the potential to influence population growth rate in this species.

Within the Cape Peninsula population, we found a sex bias in infection prevalence, with more males infected than would be expected assuming a 1:1 sex ratio. This male bias may actually be an underestimate, since ringing studies

indicate that detectability is higher for female than for male Black Sparrowhawks (Tate et al. 2017). Similar male biases in infection rates have been found in some species. For example, breeding adult male Red Crossbills (*Loxia curvirostra*) had a higher rate of infection by *K. jamaicensis* than females (Benkman et al. 2005). In contrast, however, no difference in the prevalence of infection by *K. jamaicensis* was found between the sexes of Prairie Warblers, although Benkman et al. (2005) conducted their study during the nonbreeding period, which may have had an influence (Latta 2003). Male-biased parasite prevalence has frequently been found (Roberts et al. 2004) and has been linked to the presence of hormones such as testosterone, which can suppress immune function (Folstad and Karter 1992). Behavioral traits specific to males, such as territorial disputes or reduced preening during the breeding season, may also play a role. Male Black Sparrowhawks perform most of the hunting (Tate et al. 2016) and possibly most of the territorial defense (Newton 1986) throughout the breeding season, and this greater energetic cost may put them under greater physiological stress than females, which has been linked to reduced immune function (Deerenberg et al. 1997). Indeed, in this same population, male Black Sparrowhawks infected with the blood parasite *Haemoproteus nisi* had a higher parasite load than females (Lei et al. 2013).

We found no significant difference in the incidence of infection between dark and light morphs. There may, however, have been a lack of statistical power in this test, as a result of the small sample sizes for each group. Genes coding for melanin-based plumage color have previously been shown to have pleiotropic effects (Catania and Lipton 1993, Hoekstra 2006), including providing improved parasite resistance. Indeed, in our study population, dark morphs had a higher resistance to infection by the blood parasite *H. nisi* than light morphs (Lei et al. 2013). It was suggested that the improved ability to resist chronic blood-parasite infection may explain the bias toward dark morphs in the Cape Peninsula population (Amar et al. 2013, Leit et al. 2013). In the only other study exploring ectoparasite burden in polymorphic raptors, it was found that the prevalence of the blood-sucking fly *Carnus haemapterus* in Common Buzzards (*Buteo buteo*) increased with the darkness of nestling plumage (Chakarov et al. 2008).

Close contact is likely necessary for transmission of *Knemidokoptes* between hosts (Wichmann and Vincent 1958), although some experiments have found that direct contact does not necessarily ensure transmission (Kirmse 1966). One possibility is that Black Sparrowhawks in our study population are becoming infected through infected prey. This species feeds almost exclusively on birds (Malan and Robinson 1999, Suri et al. 2016) and regularly preys on domestic fowl (Suri et al. 2016), which are known to be

infected by multiple *Knemidokoptes* species (e.g., *K. mutans*; Morishita 1996), including within the Cape Peninsula (J. L. van Velden personal observation). If this infection pathway is responsible, it may explain the male bias in infection, given that males will spend more time processing prey during the breeding season—for example, plucking the prey before providing the processed item to the female or juveniles (Brown and Brown 1979, Katzenberger et al. 2015). Males may therefore have a higher exposure risk than females.

Another possible transmission pathway may occur when infected birds transmit mites to either partners (horizontal transmission) or chicks (vertical transmission). Although there did appear to be an age bias in *Knemidokoptes* infection, given that all infected birds were adults, it is possible that chicks die or recover without the infection ever being recorded, or that symptoms develop too slowly to be recorded when they are nestlings. However, subsequent to our analysis, 2 nestlings with clinical symptoms were produced by an infected parent (A. Koeslag personal observation), which suggests that vertical transmission may occur. Parasite virulence, in terms of the host's reproductive success, tends to be greater in horizontal transmissions than in vertical transmissions, because vertically transmitted parasites are dependent on the host's reproductive success in order to be passed on to a new host, whereas horizontal parasites are relatively independent of the host's reproduction (Clayton and Tompkins 1994). Consistent with our results, a higher prevalence of *Knemidokoptes* was found in adult Eurasian Tree Sparrows (*Passer montanus*; Mainka et al. 1994), and infection by *K. jamaicensis* was found only in adult Red Crossbills (Benkman et al. 2005).

The cities of Cape Town, Port Elizabeth, and Durban were found to be the areas with the most infection events. The other infection occurrences were single reports within a very small sample size and therefore cannot give much information. Given the diversity of sites around South Africa that have been subjected to scientific study, as well as the very few records from members of the public following an appeal for records (van Velden and Amar 2013), we believe that our data probably do reflect the real situation with respect to the prevalence of *Knemidokoptes* infection within South Africa. Although 5% of the Cape Peninsula population being infected does not necessarily constitute an epizootic event, this finding is still considerable when compared to other studied populations of wild birds of prey. One explanation for the higher frequency of infection observed in the Cape Peninsula population could be the greater monitoring effort to which this population has been subjected; however, in other regions with long-term intensive monitoring, such as Nysvley, no cases were reported. It is possible that the Cape Peninsula is suboptimal habitat for Black Sparrow-

hawks, which may make this population susceptible to mite infection via physiological stress (e.g., Latta and O'Connor 2001). However, this explanation seems unlikely given the rapid colonization and population expansion seen over the past 2 decades (Martin et al. 2014a).

The reduced nesting success and productivity we observed after infection by *Knemidokoptes* may arise because the adult birds become too agitated to incubate effectively; physical irritation has previously been identified as a cause of nest failure and desertions in other bird–parasite systems (Duffy 1983, Clayton and Tompkins 1995). However, this may be less important, given that there was a male bias in infection and that males do not play a significant role in incubation. In our observations of female Black Sparrowhawks on the Cape Peninsula that exhibited signs of clinical infection, the birds appeared to be agitated, restless, and nervous of disturbance, often flying off the nest when approached. These behavioral changes will likely disturb incubation, leading to clutch failure. If the male is infected, hunting efficiency may be reduced, which may, in turn, negatively affect breeding performance. Additionally, the productivity of this species is significantly affected by nest usurpation by Egyptian Geese (*Alopochen aegyptiaca*; Curtis et al. 2007, Sumasgutner et al. 2016), and the weakened state of infected Black Sparrowhawks may potentially compromise the ability of these individuals to defend against geese or build replacement nests.

Conclusion

This is the first study of mites in the genus *Knemidokoptes* within a wild population of birds of prey. All other cases of infection by these mites occurred in lone, usually captive, birds of prey. The prevalence of this infection in the Cape Peninsula and Durban populations seems unusually high. Breeding performance was lower following mite infection than prior to it, and was lower for infected pairs than for noninfected pairs, which has the potential to affect the stability of this population over time. Males appear to be especially affected by this infection, potentially because of the greater energetic costs they bear at breeding, leading to a weakened immune system, or else from greater exposure to vectors such as infected prey. Infections in this population emerged only after the number of pairs surpassed 25, and therefore it may be a density-dependent parasite. Although the population of Black Sparrowhawks has been steadily increasing since their colonization of the Cape Peninsula, *Knemidokoptes* infections could, in theory, reduce this growth rate through the negative effect on breeding performance. Although the Black Sparrowhawk is not a species of conservation concern, an understanding of this parasite's occurrence and its effects on a wild raptor

species may prove useful should epizootic events occur in another threatened raptor population.

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