DIVERSITY AND ABUNDANCE OF NONCULICID BITING FLIES (DIPTERA) IN A ZOO ENVIRONMENT

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ABSTRACT. The diversity of nonculicid biting flies was surveyed in Sunset Zoo, Manhattan, KS, by carbon dioxide–baited traps. A total of 8,399 nonculicid biting-fly females representing 32 species and 5 families were collected. Twenty-one biting midge (Ceratopogonidae: Culicoides) and 7 black fly (Simuliidae) species were collected, including new state records of 3 Culicoides and 1 simulid. The species richness of Culicoides and Simuliiidae within the zoo represents 72.4% and 41.2%, respectively, of the fauna known to occur in Kansas. Trap type significantly influenced (P < 0.05) collections of the 5 species analyzed, and trapping period affected 3 species. The diversity and abundance of nonculicid biting flies in the zoo as related to animal health and wellness is discussed.

KEY WORDS Black flies, biting midges, Culicoides, new records, Simuliidae

INTRODUCTION

Zoological parks represent an exceptional grouping of species populations, mixing exotic and native vertebrates, humans, and arthropods in a highly heterogeneous environment. The comingling and movement of these species (transport of captive species and dispersal or migration of native species) can increase the risk of transmission of arthropod-borne enzootic and zoonotic diseases by bringing naïve and potential reservoir populations in close proximity to vectors and associated pathogens and parasites (Fix et al. 1988, McConkey et al. 1996, Ludwig et al. 2002, Alley et al. 2008). Over the past 3 decades, approximately 25 arthropod-borne diseases have been documented in zoo animals (Adler et al. 2011). Human health and well-being is of concern, as well. Zoo workers are at risk of contracting animal ectoparasites (e.g., scabies), being bitten by arthropods, or developing allergies to insects (Adler et al. 2011). Additionally, >600 million people worldwide visit zoos and aquariums annually (Gusset and Dick 2011), providing numerous opportunities for vector-borne diseases to be transmitted from zoo fauna to humans and vice versa.

Mosquitoes receive a large proportion of attention related to arthropod pests of zoo animals; attention that is rightfully deserved as mosquitoes are the most important arthropods in this regard (Adler et al. 2011). However, nonculicid biting flies are vectors of significant animal and human disease agents, and bites can induce stress in the hosts. Some species can be more abundant in zoos than in surrounding habitats (Vilar et al. 2011). Surveys of nonculicid biting flies in zoological parks include Culicoides (Ceratopogonidae) (Labuschagne et al. 2007, Nelder et al. 2010, Vilar et al. 2011) and stable flies (Muscidae) (Rugg 1982, Changbunjong et al. 2012, Ose and Hogsette 2014, Njila et al. 2015). Reports of black flies (Simuliidae) and sand flies (Psychodidae: Phlebotominae) in zoos are lacking. However, disease agents transmitted by these flies are known from zoo animals (Halpern and Bennett 1983, Rose et al. 2004, Malta et al. 2010), indicating these vectors potentially occur in zoos. Knowledge regarding horse flies and deer flies (Tabanidae) in zoos is lacking as well (Adler et al. 2011, Njila et al. 2015). In addition to acting as vectors, nonculicid biting flies undoubtedly contribute to the biting pressure experienced by zoo animals, which can negatively impact their well-being.

To better understand how biting flies affect the welfare of zoo fauna, an understanding of the flies present in zoos is needed. We investigated the species richness and abundance of these flies in a zoo environment. The objectives of this study were 2-fold: 1) survey the diversity and abundance of nonculicid biting flies in a zoo environment, and 2) assess variables associated with collection methods to identify useful parameters for improving surveillance of these flies.

MATERIALS AND METHODS

Study site

The Sunset Zoo (SSZ) is situated on 19.4 ha (48 acres) atop a hill on the west side of Manhattan, KS, a city at the confluence of the Kansas and Big Blue rivers in the Flint Hills Ecoregion (39.1795’N, 96.5920’W). The region is dominated by rolling hills and tall- and short-grass prairies growing in a thin soil layer overlaying flinty beds of limestone. The SSZ is surrounded by a city cemetery (north), the city...
high school (northeast), a forested area surrounding Wildcat Creek (west), and residential areas (south and east) (Fig. 1). The SSZ is an Association of Zoos and Aquariums–accredited zoo that houses more than 100 species and 300 individual animals of various conservation statuses.

Eight trapping sites were selected within the SSZ. These were used from March to October of 2015 to sample various zoo habitats and survey vector communities in close proximity to animal enclosures (Fig. 1). Sites were separated by 50 m or more to help ensure site independence and were positioned near the following animal enclosures or areas: quarantine building (site 1), chimpanzees (Pan troglodytes (Blumenbach)) (site 2), maintenance buildings (site 3), Australian animals and raptors (site 4), Malaysian tigers (Panthera tigris jacksoni (L.)) and red-crowned cranes (Grus japonensis (Müller)) (site 5), Kansas native animals (site 6), ungulates (site 7), and a children’s playground (site 8) (Fig. 1).

Collection methods

Centers for Disease Control and Prevention (CDC) ultraviolet light traps (Trap Model 1212; John W. Hock Company, Gainesville, FL, www.johnwhock.com) and Biogents-Sentinel (BG-S) traps (BG-1 Sentinel; Biogents, Regensburg, Germany, www.bg-sentinel.com) with BG-Lure cartridges (mixture of ammonia, lactic acid, and caproic acid) were used for collections. The CDC traps were suspended approximately 1.5 m above the ground in areas with >50% tree canopy coverage and powered by a 12-V battery. A total of 8 CDC and 7 BG-S traps (no BG-S at location 1) were used. Each trap was baited with 0.5 kg of dry ice suspended above the trap in 3.8-liter insulated container.

Collections were conducted in 2015 and initiated when ambient temperatures exceeded 15°C for 6 or more hours per day (i.e., March) and ended when temperatures dropped below this threshold for 6 or more hours per day (i.e., October). Sites were sampled during the final week of each month over 3 consecutive 24-h periods when weather permitted. In the event of inclement weather, trapping was halted and resumed for an additional 12–24 h to compensate for lost trapping time. Each 24-h period was divided into “day” (1 h prior to sunrise to 1 h after sunset) (n = 3 per month) and “night” (1 h after sunset to 1 h prior to sunrise) (n = 3 per month) treatments to capture diurnal/crepuscular and nocturnal biting-fly species, respectively. This division of day and night resulted in changing sampling periods throughout the study as photoperiod changed (e.g., day was longer in June than other months), but provided a biological rationale based on known behavior of biting flies for the divisions of night and day. Collections were retrieved at the end of each day and night period and clean collection containers installed.

Flies captured in CDC traps were collected into 70% ethanol from March to July and alive from August to October (a concurrent study from March to July required catches to be preserved in ethanol). Insects caught in BG-S traps were collected alive. Following each trapping period, catches were stored at -20°C and fixed in 70% ethanol after sorting.

Identification

Nonculicid biting flies were identified to the lowest taxonomic unit possible. Identifications of Culicoides were made using Wirth and Blanton (1967), Atchley (1970), Battle and Turner (1971), Jones and Wirth (1977), Blanton and Wirth (1979), Wirth et al. (1985), and Pappas and Pappas (1989) and confirmed by slide mounting voucher specimens of each species. Simuliidae were identified to species or species group via Adler et al. (2004). Phlebotomine psychodids were identified using Young and Perkins (1984). Tabanidae were identified to family level only. Voucher specimens were deposited in the Kansas State University Museum of Entomological and Prairie Arthropod Research and the synoptic collection of D. A. Swanson.

Data analyses

Collection variables were assessed for significant predictors of fly abundance for the 5 most abundant species, excluding Stomoxys calcitrans (L.) (58.3% of the total Stomoxys species captured was in a single trap). Because of violations of assumptions for
parametric statistics, the data were analyzed non-parametrically by rank transformation followed by analysis of variance using the factors trap type (BG-S and CDC) and trap period (day and night). Significant differences were determined at an alpha of 0.05. Results are presented as nontransformed data to provide more meaningful comparisons. All statistical analyses were performed using the R statistical platform (R Development Core Team 2010).

RESULTS

A total of 8,975 biting flies were collected in SSZ. The 8,399 females (and male stable flies) and 576 nonbiting males represented 5 families and 32 species (Table 1). Twenty-one Culicoides species were collected (Table 1). Three species, C. ousairani Khalaf, C. brookmani Root and Hoffman, and C. denningi Foote and Pratt, were new records for the state of Kansas (Borkent and Grogan 2009). At least 7 species of Simuliidae were collected (Table 1). Adults of the Simulium jenningsi group and S. tribulatum/vittatum group could not be distinguished morphologically and could increase species richness depending on group composition. One tick specimen, Amblyoma americanum (L.), was collected in a BG-S trap. The most abundant species were S. meridionale Riley (4,384; 52.2%), C. crepuscularis Malloch (1,790; 21.3%), St. calcitrans (760; 9.1%), C. guttipennis (Coq.) (332; 4.0%), C. stellifer (Coq.) (297; 3.5%), and C. haematopotus Malloch (252; 3.0%) (Table 1).

Trap type significantly affected trap collections of all 5 species analyzed, with all being collected more frequently in CDC traps (Fig. 2). Trapping period was significant for C. crepuscularis, C. haematopotus, and S. meridionale but not for C. guttipennis and C. stellifer (Fig. 3). Culicoides crepuscularis (P < 0.001) and C. haematopotus (P < 0.02) were collected in significantly higher numbers during the night period, while S. meridionale (P < 0.0001) was collected in greater abundance during the day period (Fig. 3).

DISCUSSION

Trap type and trap period were found to be significant in collection of nonculicid biting flies. Ultraviolet-lighted CDC light traps collected more of the species analyzed than BG-S traps (Fig. 2). The ultraviolet light could account for the differences in performance. Nelder et al. (2010) found that ultraviolet CDC traps performed better than incandescent CDC traps at catching biting midges in South Carolina zoos. They hypothesized the ultraviolet light was able to stand out from the background lighting and was thus more attractive. The results of the trap period analysis show biting-fly activity is occurring when humans are unlikely to notice, which is at night. Two species were most active at night and S. meridionale, collected primarily in the “day” period, is more active in the evenings when humans are likely absent from the zoo (Adler et al. 2004). These results emphasize the importance of surveillance design as animals cannot inform human caretakers of fly bites, and the activity of these species would be overlooked if left to caretaker observations and patron complaints.

Four new state records, 3 biting midge species and 1 black fly species, were collected in the SSZ. Culicoides ousairani is distributed from Pennsylvania to Oklahoma (Borkent and Grogan 2009), but to our knowledge, has not been reported from Kansas. The collections of C. brookmani and C. denningi in Kansas represent greater additions to known distributions. Culicoides brookmani is known from west Texas to California, and C. denningi from western...

### Table 1. Richness and abundance of biting flies in the Sunset Zoo by trap type. Numbers represent female counts except Stomoxys calcitrans (males and females not separated) and Lutzomyia vexator (only males collected). Taxa alphabetized within families.

| Taxon                                      | BG-S | CDC | Total |
|--------------------------------------------|------|-----|-------|
| Ceratopogonida                             |      |     |       |
| Culicoides arboricola                      | 0    | 41  | 41    |
| C. brookmani                               | 0    | 1   | 1     |
| C. crepuscularis                           | 76   | 1,714 | 1,790 |
| C. debilipalpis                            | 0    | 6   | 6     |
| C. denningi                                | 0    | 1   | 1     |
| C. elemae                                  | 0    | 14  | 14    |
| C. guttipennis                              | 24   | 308 | 332   |
| C. haematopotus                             | 1    | 251 | 252   |
| C. hiruglyphicus/jamesii                   | 1    | 1   | 2     |
| C. himani                                  | 0    | 29  | 29    |
| C. nanus                                   | 2    | 30  | 32    |
| C. obsolitus                                | 2    | 94  | 96    |
| C. ousairaini                              | 0    | 10  | 10    |
| C. paraensis                               | 0    | 13  | 13    |
| C. sanguisuga                              | 5    | 127 | 132   |
| C. sonorensis                              | 0    | 15  | 15    |
| C. stellifer                               | 5    | 292 | 297   |
| C. stomi                                   | 0    | 10  | 10    |
| C. travisi                                 | 0    | 48  | 48    |
| C. venustus                                | 0    | 1   | 1     |
| C. villosipennis                           | 1    | 0   | 0     |
| Muscidae                                   |      |     |       |
| Haematobia irritans                        | 0    | 1   | 1     |
| Stomoxys calcitrans                        | 724  | 36  | 760   |
| Psychodidae                                |      |     |       |
| Lutzomyia vexator                          | 1    | 1   | 2     |
| Simuliidae                                 |      |     |       |
| Simulium bivittatum                        | 8    | 2   | 10    |
| S. jenningsi group                         | 13   | 9   | 22    |
| S. johannseni                              | 3    | 1   | 4     |
| S. luggeri                                 | 0    | 1   | 1     |
| S. meridionale                             | 1,382 | 3,002 | 4,384 |
| S. pilosum                                 | 7    | 57  | 64    |
| S. tribulatum/vittatum                     | 5    | 23  | 28    |
| Tabanidae                                  | 0    | 2   | 2     |
| Total                                      | 2,260 | 6,141 | 8,401 |

1 BG-S, carbon dioxide–baited Biogents-Sentinel trap; CDC, Centers for Disease Control and Prevention ultraviolet light trap.

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Nebraska to Nevada north to Alberta and Saskatchewan (Atchley 1970, Borkent and Grogan 2009). The collection of singleton specimens of these species in eastern Kansas could be the result of chance dispersal events (e.g., wind or human-aided dispersal) and may or may not represent established populations in the state. The collection of *Simulium bivittatum* Malloch represents a new state record (Adler et al. 2004). *Simulium bivittatum* is known from Texas north to Alberta and Saskatchewan (Adler et al. 2004) but had not been reported in Kansas (Mock and Adler 2002). The collection of *Lutzomyia vexator* (Coq.) expands the known distribution range northward from 1 known location in southeastern Kansas (Weng et al. 2012).

A diverse number of nonculicid biting flies were collected in the SSZ. Adler et al. (2011) notes that few studies have rigorously compared biting-fly fauna within zoos to surrounding areas but biting flies within zoos are a subset of the adjacent fauna. The diversity of flies within the small area (19.4 ha, 48 acres) of SSZ is relatively high compared to surrounding statewide areas of Kansas, Missouri, and Oklahoma (Table 2). Twenty-one *Culicoides* species were collected in SSZ over a single season compared to 23 in a survey of 41 stations across Oklahoma over 3 years (Khalaf 1957) and 22 in a 2-county survey of Missouri over 2 years (Childers and Wingo 1968) (Table 2). Based on distribution records in Borkent and Grogan (2009), 26 species of *Culicoides* are predicted to occur in Kansas (Table 2). With the addition of the 3 new state records, the SSZ midge fauna would represent 72.4% (21/29) of the species found in Kansas. The high diversity of biting flies in the SSZ could be an effect of habitat and host heterogeneity within the zoo. In contrast, biting midge diversity on 10 dairy farms in Nebraska ranged from 1 to 9 species (median = 5) per farm (Swanson, unpublished data). The relatively low amount of habitat and host heterogeneity on a dairy farm versus a zoo could explain the high diversity of biting flies observed in SSZ. How fly diversity within zoos compares to adjacent areas is an area in need of further study.

The ecology of the biting flies collected reveals a vector community originating from a mixture of habitats. *Culicoides* breed in various wet or moist habitats and some species are capable of dispersing 1–4 km from release points (Lillie et al. 1985, Kirkeby et al. 2013, Kluiters et al. 2015). Black flies breed in flowing water, but little permanent flowing water is available on-site at the SSZ. The nearest source of flowing water is Wildcat Creek, which runs adjacent to the SSZ, but the likely major source of black flies is the Kansas River 2.5 km (at its nearest point) from the zoo. The dispersal ability of black flies is much greater than *Culicoides*. *Simulium meridionale* has been reported to travel 30 km from larval habitats (Fredeen 1956). Therefore, the biting-fly community at the SSZ is composed of *Culicoides* breeding in multiple habitats on-site and/or in surrounding areas, while the black flies originate from off-site locations. The interchange of biting flies into and out of the SSZ could facilitate the transfer of vector-borne disease agents to or from the zoo fauna.

The effect of biting-fly diversity on the health and welfare of the zoo animals is of potential concern as it has the potential to affect the animals in numerous ways. From a disease standpoint, transmission dynamics of vector-borne pathogens can depend on multiple factors, including host specificity of vectors, proportion and abundance of competent reservoir hosts, and dilution effects due to host diversity (Ostfeld and Keesing 2000, Keesing et al. 2006). The diverse number of biting-fly species could allow more opportunities for various disease agents to be...
Several species of flies were collected in relatively higher numbers than others. The biological or epidemiological implications of larger populations of these species in the zoo is not known, but those more abundant species are known pests and/or vectors. *Stomoxys calcitrans* is a large, conspicuous species inflicting painful, stress-inducing bites that can cause physical damage to hosts (e.g., blisters and lesions) (Schwinghammer et al. 1987, Catangui et al. 1993, Mock and Adler 2002, Adler et al. 2004, Schnellbacher et al. 2012). This species also bites humans and other mammals (Mock and Adler 2002).

Black flies and *Culicoides* have not been reported as a problem within the SSZ likely because they are most active in crepuscular and nocturnal time periods, when zoo patrons and staff are absent (zoo closes at 1700 h). Further investigations should be conducted as to how these flies affect the zoo fauna.

Captive zoo fauna are exposed to a great diversity of biting flies beyond mosquitoes. To monitor these flies, the appropriate strategies need to be employed. We found that CDC ultraviolet light traps functioned significantly better at collecting nonculicid biting flies than BG-S traps. The timing of trapping was important as well, with *Culicoides* being collected more in the night period and black flies more in the day period. The high proportion of the biting-fly fauna collected in the zoo may be a result of the diversity of habitats and hosts within the zoo but needs further investigation. The diversity of flies collected suggests zoos can be important surveillance points for vectors. Surveys should be conducted to document the hosts and breeding habitats of nonculicid biting flies in and around zoos, investigating the negative effects flies have on zoo animals (e.g., stress, behavioral changes), and assessing the need for vector management programs for these pests.

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**Table 2. Comparisons of *Culicoides* and Simuliidae species richness in Sunset Zoo relative to species richness of selected states and studies.**

| Taxon     | Sunset Zoo | Kansas          | Oklahoma | Missouri |
|-----------|------------|-----------------|----------|----------|
| *Culicoides* | 21         | 26 predicted¹ | 27 predicted¹ | 27 predicted¹ |
| Simuliidae | 7          | 16²            | 12⁴      | 14⁴      |

¹ Predictions of species richness made from distribution ranges of Borkent and Grogan (2009).
² Survey based on results of Khalaf (1957).
³ Survey based on results of Childers and Wingo (1968).
⁴ Richness based on distributions of Adler et al. (2004).

transmitted between feral and captive animals. *Culicoides* species collected in this study are known or suspected vectors of avian malaria (*Haemoproteus*), bluetongue virus, and epizootic hemorrhagic disease virus in the USA (Mullen 2009). Black fly species collected in this study have been incriminated as vectors of *Leucocytozoon* (Adler and McCreadie 2009). Physical injuries can occur due to bites from nonculicid biting flies and lead to secondary excoriations or ulcerative lesions. These injuries can lead to infections or scar tissue, negatively impacting animal well-being and reducing the attractiveness of animals on display (Njila et al. 2015). In terms of behavior, animals may partake in more defensive behaviors at the expense of feeding or resting in response to high biting pressure (Ralley et al. 1992, Toupin et al. 1996). From a physiological standpoint, bites from hematophagous insects can elevate stress levels (Schwinghammer et al. 1987, Catangui et al. 1997, Martínez-de la Puente et al. 2011, López-Arrabé et al. 2015), induce allergic reactions (Mullen 2009), or cause toxic shock. Stressed hosts can be more vulnerable to biting flies (Gervasi et al. 2016) and disease (Lafferty and Holt 2003). Aside from directly affecting zoo animal health and well-being, nonculicid biting flies could indirectly affect hosts by inducing stress, making hosts more vulnerable to mosquitoes and mosquito-borne diseases.

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**REFERENCES**

Adler and McCreadie 2009

Catangui et al. 1997

Childers and Wingo 1968

Khalaf 1957

Mullen 2009

Mock and Adler 2002

Schwinghammer et al. 1987

Toupin et al. 1996

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REFERENCES CITED

Adler PH, Currie DC, Wood DM. 2004. The black flies (Simuliidae) of North America. Ithaca, NY: Cornell Univ. Press.

Adler PH, McCreadie JW. 2009. Black flies (Simuliidae). In: Mullen GR, Durden LA, eds. Medical and veterinary entomology. 2nd edition. New York, NY: Academic Press. p 189–206.

Adler PH, Tuten HC, Nelder MP. 2011. Arthropods of medicoveterinary importance in zoos. Annu Rev Entomol 56:123–142.

Alley MR, Fairley RA, Martin DG, Howe L, Atkinson T. 2008. An outbreak of avian malaria in captive yellow-heads/mohua (Mohua ochrocephala). NZ Vet J 56:247–251.

Atchley WR. 1970. A biosystematic study of the subgenus Selfia of Culicoides (Diptera: Ceratopogonidae). Univ Kansas Sci Bull 49:181–336.

Battle FV, Turner EC Jr. 1971. A systematic review of the genus Culicoides (Diptera: Ceratopogonidae) of Virginia with a geographic catalog of the species occurring in the eastern United States north of Florida. Research Division Bulletin 44. Blacksburg, VA: Virginia Polytechnic Institute and State Univ. 129 p.

Blanton FS, Wirth WW. 1979. The sand flies (Culicoides) of Florida (Diptera: Ceratopogonidae). In: Arthropods of Florida and neighboring land areas. Volume 10. Gainesville, FL: Florida Department of Agriculture and Consumer Services. p 1–204.

Borkent A, Grogan WL Jr. 2009. Catalog of the new world biting midges north of Mexico (Diptera: Ceratopogonidae). Zootaxa 2273:1–48.

Catangui MA, Campbell JE, Thomas GD, Boxler DJ. 1997. Calculating economic injury levels for stable flies (Diptera: Muscidae) on feeder heifers. J Econ Entomol 90:6–10.

Changbunjong T, Weluwanarak T, Ratanakorn P, Maneeon S, Sriwhichai P, Sumruayphol S, Ruangsittichai J. 2012. Distribution and abundance of Stomoxyini flies (Diptera: Muscidae) in Thailand. Southeast Asian J Trop Med Public Health 43:1400–1410.

Childers CC, Wingo CW. 1968. Genus Culicoides (Diptera: Ceratopogonidae) in central Missouri. Species; seasonal abundance; activity. Res Bull Mo Agric Exp Stn 934:1–32.

Fix AS, Waterhouse C, Greiner EC, Stoskopf MK. 1988. Plasmodium relictum as a cause of avian malaria in wild-caught Magellanic penguins (Spheniscus magellanicus). J Wildl Dis 24:610–619.

Freedon FJH. 1956. Research on black flies, pests of livestock and man on the Canadian prairies. Proc Entomol Soc Mani 12:2–10.

Gervasi SS, Burkett-Cadena N, Burgan SC, Schrey AW, Hassan HK, Unnasch TR, Martin LB. 2016. Host stress hormones alter vector feeding preferences, success, and productivity. Proc Biol Sci 283:201612278.

Gusset M, Dick G. 2011. The global reach of zoos and aquariums in visitor numbers and conservation expenditures. Zoo Biol 30:566–569.

Halpern N, Bennett GF. 1983. Haemoproteus and Leucocytozoon infections in birds of the Oklahoma City Zoo. J Wildl Dis 19:330–332.

Jones RH, Wirth WW. 1977. A new species of western Culicoides of the stonei group (Diptera: Ceratopogonidae). Entomol News 89:56–58.

Keeling F, Holt RD, Ostfeld RS. 2006. Effects of species diversity on disease risk. Ecol Lett 9:485–498.

Khalaf KT. 1957. Light-trap survey of the Culicoides of Oklahoma (Diptera, Heleidae). Am Midl Nat 58:182–221.

King RS, Adler PH. 2012. Development and evaluation of methods to assess populations of black flies (Diptera: Simuliidae) at nests of the endangered whooping crane (Grus americana). J Vector Ecol 37:298–306.

Kirkeby C, Bodker R, Stockmarr A, Lind P, Heegaard PMH. 2013. Quantifying dispersal of European Culicoides (Diptera: Ceratopogonidae) vectors between farms using a novel mark-release-recapture technique. PLoS ONE 8:e61269.

Kluters G, Swales H, Baylis M. 2015. Local dispersal of Palearctic Culicoides biting midges estimated by mark-release-recapture. Parasit Vectors 8:86.

Labuschagne K, Gerber LJ, Espie I, Carpenter S. 2007. Culicoides biting midges at the National Zoological Gardens of South Africa. Onderstepoort J Vet Res 74:343–347.

Lafferty KD, Holt RD. 2003. How should environmental stress affect the population dynamics of disease? Ecol Lett 6:654–664.

Lillie TH, Kline DL, Hall DW. 1985. The dispersal of Culicoides mississippiensis (Diptera: Ceratopogonidae) in a salt marsh near Yankeetown, Florida. J Am Mosq Control Assoc 1:463–467.

López-Arrabé J, Cantarero A, Pérez-Rodríguez L, Palma A, Alonso-Alvarez C, González-Brajos S, Moreno J. 2015. Nest-dwelling ectoparasites reduce antioxidant defences in females and nestlings of a passerine: a field experiment. Oecologia 179:29–41.

Ludwig GV, Calle PP, Mangiafico JA, Raphael BL, Danner DK, Hile JA, Clippinger TL, Smith JF, Cook RA, McNamara T. 2002. An outbreak of West Nile virus in a New York City captive wildlife population. Am J Trop Med Hyg 67:67–75.

Malta MCC, Tinoco HP, Xavier MN, Vieira ALS, Costa EA, Santos RL. 2010. Naturally acquired visceral leishmaniasis in nonhuman primates in Brazil. Vet Parasitol 169:193–197.

Martínez-de la Puente J, Merino S, Moreno J, Morales J, Lobato E, Martínez I. 2011. Nest ectoparasites increase physiological stress in breeding birds: an experiment. Naturwissenschaften 98:99–106.

McConkey GA, Li J, Rogers J, Seeley DC Jr, Graczyk TK, Cranfield MR, McCutchan TF. 1996. Parasite diversity in an endemic region for avian malaria and identification of a parasite causing penguin mortality. J Eukaryot Microbiol 43:393–399.

Mock DE, Adler PH. 2002. Black flies (Diptera: Simuliidae) of Kansas: review, new records, and pest status. J Kans Entomol Soc 75:203–213.

Mullen GR. 2009. Biting midges (Ceratopogonidae). In: Mullen GR, Durden LA, eds. Medical and veterinary entomology. 2nd edition. New York, NY: Academic Press. p 169–188.

Nelder MP, Swanson DA, Adler PH, Grogan WL Jr. 2010. Biting midges of the genus Culicoides in South Carolina zoos. J Insect Sci 10:55.

Njila HL, David S, Ombudagad A. 2015. Prevalence of biting and non-biting flies in relation to species in the Jos
Museum Zoological Garden, north central Nigeria. Bayero J Pure Appl Sci 8:149–152.

Ose GA, Hogsette JA. 2014. Spatial distribution, seasonality and trap preference of stable fly, Stomoxys calcitrans L. (Diptera: Muscidae), adults on a 12-hectare zoological park. Zoo Biol 33:228–233.

Ostfeld RS, Keesing F. 2000. The function of biodiversity in the ecology of vector-borne zoonotic diseases. Can J Zool 78:2061–2078.

Pappas CD, Pappas LG. 1989. Culicoides elemae, a new species in the Culicoides guttipennis species group (Diptera: Ceratopogonidae). J Kans Entomol Soc 62:228–233.

Ralley WE, Galloway TD, Crow GH. 1992. Individual and group behaviour of pastured cattle in response to attack by biting flies. Can J Zool 71:725–734.

R Development Core Team. 2010. R: a language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing [accessed May 31, 2010]. Available from: http://www.R-project.org.

Rose K, Curtis J, Baldwin T, Mathis A, Kumar B, Sakthianandeswaren A, Spurck T, Low Choy J, Handman E. 2004. Cutaneous leishmaniasis in red kangaroos: isolation and characterisation of the causative organisms. Int J Parasitol 34:655–664.

Rugg D. 1982. Effectiveness of Williams traps in reducing the numbers of stable flies (Diptera: Muscidae). J Econ Entomol 75:857–859.

Sanford D, Eikenhorst B, Lamb T, Cates JE, Robinson J, Olsen J, Hoelscher C, Jeffrey J. 1993. Black flies cause costly losses in East Texas ostriches and emus. Texas Agric Ext Serv Vet Quart Rev 9:1–2.

Schnellbacher RW, Holder K, Morgan T, Foil L, Beaufrère H, Nevarez J, Tully TN Jr. 2012. Avian simuliosis: outbreak in Louisiana. Avian Dis 56:616–620.

Schwinghammer KA, Knapp FW, Boling JA. 1987. Physiological and nutritional response of beef steers to combined infestations of horn fly and stable fly (Diptera: Muscicidae). J Econ Entomol 80:120–125.

Toupin B, Huot J, Manseau, M. 1996. Effect of insect harassment on the behaviour of the Rivièrè George Caribou. Arctic 49:375–382.

Vilar MJ, Guis H, Krzywinski J, Sanderson S, Baylis M. 2011. Culicoides vectors of bluetongue virus in Chester Zoo. Vet Rec 168:242.

Weng J, Young SL, Gordon DM, Claborn D, Petersen C, Ramalho-Ortigao M. 2012. First report of phlebotomine sand flies (Diptera: Psychodidae) in Kansas and Missouri, and a PCR method to distinguish Lutzomyia shannoni from Lutzomyia vexator. J Med Entomol 49:1460–1465.

Wirth WW, Blanton FS. 1967. The North American Culicoides of the guttipennis group (Diptera: Ceratopogonidae). Fla Entomol 50:207–232.

Wirth WW, Dyce AL, Peterson BV. 1985. An atlas of wing photographs, with a summary of numerical characters of the Nearctic species of Culicoides (Diptera: Ceratopogonidae). Contrib Am Entomol Inst 22:1–46.

Young DG, Perkins PV. 1984. Phlebotomine sandflies of North America (Diptera: Psychodidae). Mosq News 44:263–304.