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Insect-repelling behaviour in bovids: role of mass, tail length, and group size

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Biting insects are costly to hosts, and insect-repelling movements of the tail, ears, head, and feet are widespread in mammals and effective in reducing bites. We investigate whether the 'peripheral stimulation model' can explain the regulation of this widespread behaviour pattern in a comparative study of bovids. The peripheral stimulation hypothesis predicts: (1) a positive association between insect-repelling rates and body size because larger hosts produce more of the sensory cues that attract biting insects; (2) that individuals in larger groups will exhibit a higher rate of insect defense behaviour if group size and insect attraction follows a linear function; and (3) larger species will evolve proportionately longer tails in response to higher rates of insect attack. To test these predictions, we observed insect-repelling behaviour in 26 species of bovids at a zoological park, and controlled for common ancestry with formal phylogenetic analyses (independent contrasts). Consistent with the peripheral stimulation hypothesis, rates of tail-switching and all insect-repelling behaviours combined were positively associated with body mass, whereas ear-flicking was positively associated with proportional tail length. Larger bovids had proportionately longer tails for more effective fly swatting. There was no significant association between insect-repelling rate and group size, suggesting that a nonlinear relationship exists between group size and insect attacks whereby individuals in larger groups do not experience an increased attack rate. *Biological Journal of the Linnean Society*, 2007, **91**, 383–392.

ADDITIONAL KEYWORDS: biting insects – body size – Diptera – peripheral stimulation – stimulus-driven.

INTRODUCTION

Biting insects impose a number of costs on ungulate hosts, including blood loss, decreased feeding or resting time caused by disturbance, and disease transmission (Hart, 1990, 1994; Mooring & Hart, 1992; Allan, 2001; Mooring *et al.*, 2003). For example, tabanids (e.g. horse flies and deer flies) inflict a painful bite that removes as much as 0.5 mL of blood per fly (Allan, 2001). A horse may be bitten by as many as 4000 horse flies in a day, resulting in the loss of 500 mL of blood (Tashiro & Schwardt, 1949, 1953; Foil & Foil, 1988). Excessive blood-feeding by black flies can result in death to wildlife and domestic animals by exsanguination and toxic salivary secretions (Fredeen, 1973). In addition to the direct costs of blood loss, animals lose feeding time when they must repeatedly interrupt foraging to repel insects (Brindley, Bullock & Maisels, 1989). Harassment by biting insects decreases feeding and resting time in caribou and reindeer (*Rangifer tarandus* Hamilton-Smith), feral goats, and cattle, and increases time spent standing and moving (Espmark, 1967; Downes, Theberge & Smith, 1986; Brindley *et al.*, 1989; Baylis, 1996; Toupin, Huot & Manseau, 1996; Morschel & Klein, 1997). Loss of feeding time and increased energy expenditure results in a loss of weight gain for growing cattle (Harvey & Launchbaugh, 1982; Hart, 1990; Wieman *et al.*, 1992). Many biting insects are also

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*Corresponding author. E-mail: mikemooring@pointloma.edu vectors of diseases that can be transmitted to wild and domestic hosts (Allen, 1980; DeVos, 1993; Allan, 2001; Howerth, Stallknecht & Kirkland, 2001).

To reduce the pain, blood loss, and other costs of insect bites, ungulates use a varied arsenal of behaviours to repel or dislodge biting insects, including tail switching, ear flicking, head shaking, foot stamping, and muscle twitching (Hart, 1990, 1994; Moore, 2002; Mooring *et al*., 2003). A range of evidence indicates that insect-repelling activities are effective in removing flies and reducing the cost of insect attacks: (1) animals experimentally treated with insecticides to reduce insect attacks displayed fewer insect-repelling responses (Harvey & Launchbaugh, 1982; Harris, Hillerton & Morant, 1987; Woollard & Bullock, 1987; Ralley, Galloway & Crow, 1993); (2) the proportion of biting insects able to blood feed was negatively associated with the rate of insect-repelling movements (Baylis, 1996; Torr & Mangwiro, 2000); and (3) cattle suffered greater insect numbers when restrained from tail-switching by docking (Ladewig & Matthews, 1992; Eicher *et al*., 2001).

To our knowledge, a model for the proximate regulation of insect-repelling behaviour has not previously been proposed. As a starting point, we presume that some insect-repelling behaviour is evoked by the cutaneous pain of insect bites and the associated visual and auditory stimuli of biting insects, which we term ‘peripheral stimulation’. Under the ‘peripheral stimulation hypothesis’ (Table 1), we predict that: (1) hosts of larger body size will engage in a higher rate of insect-defence movements compared with smaller hosts. Because biting insects use visual, olfactory, and thermal cues to orientate to hosts (Allan & Stoffolano, 1986; Gibson, 1992; Davis & Bowen, 1994; Jordan, 1995; Spath, 1995, 1997; Mohmed-Ahmed & Mihok, 1999; Allan, 2001), and larger hosts produce more of these cues, larger animals should attract more insects and, consequently, engage in more frequent insect-repelling movements. (2) Because larger groups produce more visual, olfactory, and thermal cues that attract insects, gregarious species should attract more biting insects than more solitary species under certain conditions. If the function between group size and the attraction of biting insects is linear (individuals in larger groups experience an increased rate of insect attack), individuals in larger groups should perform more frequent insect-defence behaviours. On the other hand, if the function is nonlinear such that per capita attack rate remains constant or declines in larger groups, then individuals in larger groups will not exhibit an elevated rate of insect-defence. (3) Larger ungulates will evolve proportionately longer tails than smaller species to more efficiently repel the greater numbers of biting flies attracted to them by swatting a larger area of the body (Siegfried, 1990). Thus, longer-tailed hosts should also exhibit higher rates of insect-repelling.

The present study aimed to examine the influence of body size and grouping on insect-repelling behaviour and proportional tail length of ungulates to test the predictions of the peripheral stimulation model. Focusing on Dipteran insects (flies), we observed insect-defence rates of members of 26 species of bovids in a zoological park where the habitat was similar throughout the park. Because of the large distances between observers and animal subjects, it was not possible to collect data on insect abundance. We made the assumption that insect-repelling behaviour was a response to insect harassment (Keiper & Berger, 1982; Mooring *et al*., 2003), and that the rate of insect repelling tracked the abundance of biting insect attacks. Many previous studies have found that the frequency of insect defence behaviours is positively correlated

Table 1. Assumptions and predictions of the peripheral stimulation hypothesis for the proximate regulation of insect-repelling behaviour

Assumptions	Predictions following from assumptions
1. Larger body sized hosts will attract a higher rate of biting insect attacks compared with smaller hosts, thus will experience more cutaneous irritation	1A. *Behaviour:* Larger body sized hosts will perform a higher rate of insect-repelling compared with smaller hosts 1B. *Morphology:* Larger body sized hosts will evolve proportionately longer tails than smaller hosts to more efficiently repel insects 1C. *Behaviour:* Assuming 1B, longer-tailed hosts will perform a higher rate of insect-repelling compared with shorter-tailed hosts
2. Hosts in larger groups will attract a higher per capita rate of insect attacks compared with hosts in smaller groups, thus will experience more cutaneous irritation	2A. *Behaviour:* Hosts in larger groups will perform a higher rate of insect-repelling compared with hosts in smaller groups

with insect numbers and severity of attack (Harvey & Launchbaugh, 1982; Harris *et al*., 1987; Raymond & Rousseau, 1987; Brindley *et al*., 1989; Dougherty *et al*., 1993a, b, c, 1994, 1995; Ralley *et al*., 1993; Eicher *et al*., 2001; Mooring *et al*., 2003). Thus, we interpret insect-repelling rate as a surrogate measure of per capita insect harassment. In the present study, we used the comparative method to examine the influence of body size and grouping on insect defence behaviour. Because a given trait may be the result of common ancestry or common selection pressures, formal phylogenetic analyses were used to incorporate phylogenetic relationships among species by calculating independent contrasts and then fitting multiple regression models on these contrasts. We also conducted a morphometric analysis to determine the measure of proportional tail length most strongly associated with body size, and then included that measure as an additional factor in the multiple regression model.

MATERIAL AND METHODS

BEHAVIOURAL OBSERVATIONS

Behavioural observations were conducted on adult females of 26 species of the family Bovidae (see Appendix 1). Observations were made at the San Diego Wild Animal Park (SDWAP) from 18 May to 19 July 2001. The specific binomial or subspecific trinomial and common name of each species (as assigned by the Zoological Society of San Diego) are listed in Appendices 1 and 2. Most species were housed in large, naturalistic exhibits with many other species from the same geographical region. The animals in the large exhibits were free to graze *ad libitum* on Kikuyu grass (*Pennisetum caldenisetum*); all animals were fed alfalfa hay (*Medicago sativa*) and fibre herbivore pellets. Further information on the study site is provided in Mooring *et al*. (2000, 2002).

Observations were conducted from lookout points overlooking the exhibits using ×15–60 zoom spotting scopes mounted on tripods and ×10 binoculars at a distance of 50–200 m from the subjects. Because the abundance and attack rate of dipterans is known to increase with ambient temperature up to a point (Hughes, Duncan & Dawson, 1981; Morschel, 1999; Cepeda-Palacios & Scholl, 2000), observations were made between 10.00 h and 12.00 h, when ambient temperature reached or exceeded 25 °C. Because insect numbers and landing rates on hosts fall on windy days (Espmark, 1967; Hughes *et al*., 1981; Keiper & Berger, 1982; Downes *et al*., 1986; Morschel, 1999; Cepeda-Palacios & Scholl, 2000), observations were conducted when wind speed was calm or light (< 15 kph). Focal animals were observed only when standing up because tail switching and foot stamping cannot be performed when recumbent. With one exception, all animals were individually recognizable by ear notches and ear tags. As we were unable to distinguish the ear notches of lowland wisent (*Bison bonasus*) due to hairy ears, we conducted observations on females chosen at random from the herd.

The insect-repelling behaviours recorded were tail switches, ear flicks, head shakes, and foot stamps. During observations, we recorded the number of insect-repelling movements performed during 3-min focal animal observations (Altmann, 1974); we conducted three focal observations for each focal animal, each observation made on a separate day. Usually, we were able to observe two insect-repelling modes simultaneously (e.g. tail switching and head shaking, ear flicking and foot stamping). For tail-switching, we recorded the number of times the tail moved off-centre to the rump or back and returned; ear flicks were recorded by counting the number of times the ear nearest to the observer was flicked; head shakes involved the number of movements of the head over to the shoulder or flank and back again; for foot stamps, we recorded the number of times a leg was raised and stamped down again. The 3-min sampling sessions were timed using watches with a repeating alarm function programmed to beep at 3-min intervals, and insect-repelling movements were counted with hand tallies. Insects observed on hosts were primarily Dipterans. We calculated mean insect-repelling rates for each focal animal, and used the mean of all conspecifics as an index of species-typical, insect-repelling rate. The mean rates of insect-repelling movements performed by females of the 26 species are listed in Appendix 1.

Following a period of training, interobserver reliability tests (Caro *et al*., 1979) were conducted among all four observers (MSM, DDR, JMN, and ERO). Observers focused on the same focal animal at the same time and recorded the number of insect-repelling movements during 3-min samples. The mean Pearson correlation coefficient was very high at $r = 0.99$ for tail-switches and ear flicks (Tail switches: $N = 11$, $r = 0.972–0.999$, mean = 0.989; Ear flicks: $N = 10$, $r = 0.985–0.997$, mean = 0.991); the infrequent occurrence of head shakes and foot stamps precluded reliability analysis. Observations were completed on 303 females.

MORPHOMETRIC DATA

We collected morphological data for adult females of the same 26 species involved in the behavioural observations, drawing upon information provided in Grzimek (1968), Haltenorth & Diller (1980), MacDonald (1984), Gurung & Singh (1996), Kingdon (1997), and Nowak (1999). For each species, the following morphometric data were gathered from the literature for females: mass (kg); shoulder height from the ground, tail length (including hair tuft), and head–body length (cm); from these, we calculated the ratio of tail length to head–body length (see Appendix 1). In addition, using the method of Siegfried (1990), we used vernier calipers to measure the length of the neck, head, tail, flank, and shoulder height in relative units (cm) from photographs or figures of the animal in profile, and then calculated tail/flank and tail/shoulder ratios (see Appendix 1). Appendix 1 also contains the typical group size for each species observed at SDWAP. Because conspecifics tended to stay together in the same group, the number of individuals in the collection of each species was representative of group size.

Body mass was highly correlated with shoulder height (Pearson correlation: $N = 38$, $r = 0.89$, $P = 0.0001$) and head–body length ($N = 38$, $r = 0.83$, $P = 0.0001$); therefore, we used body mass as an index of body size. Absolute tail length increased with increasing body mass (Pearson correlation: $N = 38$, $r = 0.79$, $P = 0.0001$). All measures of proportional tail length were correlated with body mass (Pearson correlation: tail/head–body, $N = 38$, $r = 0.48$, $P = 0.002$; tail/flank, $N = 38$, $r = 0.38$, $P = 0.02$; tail/shoulder, $N = 38$, $r = 0.42$, $P = 0.01$).

STATISTICAL ANALYSIS

The phylogenetic tree used for this study (Fig. 1) was modified from a composite tree previously constructed by Mooring, Blumstein & Stoner (2004). Given the lack of consensus among previously published phylogenetic studies for ungulate species, we developed our tree based on the most recent, comprehensive, molecular studies and supplemented these data with taxonomies and studies based on morphological traits; for details, see Mooring *et al*. (2003). Using the available data, the phylogeny described above, and the computer program Compare, version 4.4 (Martins, 2001), we set all branch lengths to 1.0 (which assumes a punctuational model of evolution) and calculated phylogenetically-independent contrasts (Felsenstein, 1985; Harvey & Pagel, 1991). We then regressed independent contrasts of the independent variables (mass, tail/flank ratio, group size) against contrasts of the dependent variables (number of movements of tail, ear, and all insect-repelling modes combined per 3 min, and proportional tail length).

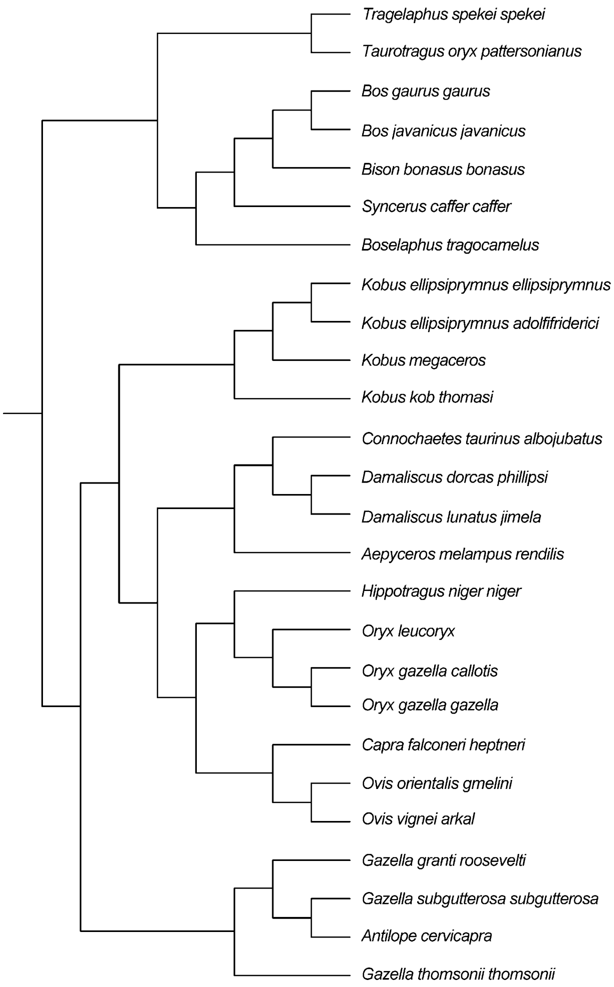

Figure 1. The phylogenetic tree used in the present study, modified from the composite tree of Mooring *et al*. (2004).

Using independent contrasts, we used a backward stepping multiple regression algorithm to determine whether measures of body size explained variation in rates of grooming. Specifically, we first entered all three main effects (mass, tail/flank, group size) along with all possible interactions. If the model *P*-value was significant, we interpreted this model. Otherwise, we systematically deleted the term that was least significant until we had a significant model and then interpreted those results. Regressions were fitted in SPSS, version 11 (SPSS Inc., Chicago, Illinois). Because independent contrasts were standardized with a mean of 0, regressions were forced through the origin (Garland, Harvey & Ives, 1992; Purvis & Rambaut, 1995). For measures of group size and tail/flank, we took independent contrasts of the log-transformed values prior to submitting to regression analysis.

RESULTS

PHYLOGENETIC ANALYSIS

Morphometric analysis

We incorporated common ancestry among species to formally examine morphometric relationships. To investigate the relationship between body size and tail length, we fitted bivariate regressions between independent contrasts of each measure of body size (mass, shoulder height, head–body length) against contrasts of each measure of proportional tail length (tail/head–body, tail/shoulder, tail/flank). Mass was positively associated with tail/shoulder (bivariate regression: $r = 0.40$, $P = 0.04$) and tail/flank ($r = 0.46$, $P = 0.02$); shoulder height was positively associated with tail/flank ($r = 0.43$, $P = 0.03$); and head–body length was positively associated with tail/flank ($r = 0.58$, $P = 0.002$). Because tail/flank was most strongly associated with body size, we used it as the measure of proportional tail length in the phylogenetic behavioural analyses.

Behavioural analysis

The mean rates of insect-repelling movements performed by females of the 26 bovid species are listed in Appendix 2. We fitted multiple regressions between independent contrasts of all three independent variables (mass, tail/flank, group size) and all possible interactions against contrasts of each of the 3 insect-repelling measures (tail, ear, all). Table 2 illustrates the final models following the backwards-stepping algorithm. After explaining variation accounted for by other terms, there was a significant, positive relationship between tail switching and mass (partial $r^2 = 0.25$, $P = 0.02$). Similarly, evolutionary increases in ear flicking were associated with evolutionary gains in tail/flank size (partial $r^2 = 0.27$, $P = 0.01$). And, larger animals engaged in more fly repelling behaviours than smaller ones (partial $r^2 = 0.22$, $P = 0.04$).

Table 2. Final regression models from the analyses of phylogenetically-independent contrasts of insect-repelling behaviours (tail-switching, ear-flicking, all behaviours combined) against contrasts of mass, tail/flank, group size, and their interactions

	Source d.f.	F	P	Partial r^2
Tail-switching				
Model	6	2.96	0.033*	0.483
Mass	1	6.27	0.022*	0.248
Group size × tail/flank	1	2.47	0.132	0.115
Group size	1	1.43	0.247	0.070
Tail/flank	1	1.10	0.308	0.055
Mass × tail/flank	1	0.24	0.633	0.012
Mass × group size	1	0.12	0.732	0.006
Ear-flicking				
Model	3	3.48	0.033*	0.322
Tail/flank	1	8.32	0.009*	0.274
Mass × tail/flank	1	2.98	0.099	0.119
Group size	1	1.52	0.231	0.065
All insect-repelling combined				
Model	7	2.74	0.040*	0.516
Mass	1	5.05	0.037*	0.219
Tail/flank	1	2.83	0.110	0.136
Group size	1	0.58	0.456	0.031
Group size × tail/flank	1	0.55	0.469	0.029
Mass × group size	1	0.21	0.651	0.012
Mass × group size × tail/flank	1	0.08	0.783	0.004
Mass × tail/flank	1	0.04	0.836	0.002

*Significant P-values. $N = 26$ bovid species.
d.f., degrees of freedom.

DISCUSSION

MORPHOMETRIC ANALYSIS

Phylogenetic analyses indicated that body size was positively associated with proportional tail length for Bovidae, as predicted by the peripheral stimulation model. These results indicate that, with phylogeny accounted for, larger species of bovids have proportionately longer tails, as previously reported by Siegfried (1990) for African bovids in a study in which phylogeny was not accounted for. The ‘tail switching hypothesis’ of Siegfried (1990) proposed that small species of African ungulates tend to inhabit dense vegetation in which a long tail is a liability, and thus are predicted to have proportionately shorter tails compared with larger species. Siegfried (1990) further proposed that large African ungulates tend to inhabit open habitat in which tails are not a liability, and thus will have proportionately longer tails. The latter prediction assumed that a long tail is the most energetically efficient arrangement for larger ungulates (i.e. uses less energy than movements of legs or head). Although many studies have concluded that there is a general trend of smaller ungulates being associated with closed habitats and large ungulates being associated with open habitat (Jarman, 1974; Perez-Barberia, Gordon & Pagel, 2002), the liability of short tails and the energetic efficiency of long tails remain untested. Another speculated explanation for proportionately longer tails in larger ungulates is that tails may be used as a visual signal that would be facilitated in the open habitat typical of larger species (Kiley-Worthington, 1976; Hirth & McCullough, 1977; Hickman, 1979; Walther, 1984).

We propose that the main reason larger bovids have longer tails is that they tend to attract more biting flies to them, and longer tails are more efficient fly swatters because they repel insects over a broader area of the body surface. This is supported by our behavioural results. Thus, longer tails may have evolved primarily as an adaptation to higher rates of insect attack on larger-bodied bovids, in accordance with the peripheral stimulus model.

INSECT-REPELLING BEHAVIOUR

For Bovidae, body mass was positively correlated with rates of tail-switching and all insect-repelling combined, whereas tail/flank ratio was positively associated with body mass and ear flicking rate. These results indicate that larger, longer-tailed bovids used more frequent insect-repelling movements to defend themselves against biting flies, as predicted by the peripheral stimulation model.

Host-seeking haematophagous (blood-feeding) insects use visual cues (such as size, contrast, colour, and pattern), airborne chemical cues found in host breath (carbon dioxide, acetone, octenol), urine (phenols), faeces, and skin, and/or body heat of endothermic hosts to locate suitable hosts (Allan & Stoffolano, 1986; Gibson, 1992; Davis & Bowen, 1994; Jordan, 1995; Spath, 1995, 1997; Mohmed-Ahmed & Mihok, 1999; Allan, 2001). Larger-bodied bovids should be more attractive to biting insects because they present a larger visual image and produce more airborne odourants and heat than smaller bovids (Collins & Urness, 1982), and therefore should defend themselves by performing insect-defence movements more frequently than smaller bovids.

Group size was not significantly associated with any insect-repelling behaviours, contrary to the prediction of the peripheral stimulation model. However, the prediction assumes a linear function between group size and insect attack rate. It appears likely that group size and attack rate exhibit a nonlinear function, meaning that the per capita rate of insect attack either declines or remains constant with change in group size. Some previous studies have indicated that bunching behaviour can dilute the number of per capita insect attacks on animals (Espmark, 1967; Hansens & Valiela, 1967; Schmidtmann & Valla, 1982; Schmidtmann, 1985; Rutberg, 1987; Wieman *et al*., 1992; Mooring *et al*., 2003) and artificial traps (Helle & Aspi, 1983). However, in the present study, neither a positive, nor a negative association of group size with insect-repelling rate was found.

Our findings indicate that at least some aspects of bovid insect-defence behaviour are stimulus-driven, evoked directly from cutaneous irritation caused by insect bites. The results of the comparative study indicated that, with phylogenetic relationship controlled for, larger bovids attracted more insects, and the increased density of insect attacks stimulated higher rates of insect repelling behaviour and the evolution of longer tails. Because insect-repelling rates increased with body size, the peripheral stimulation model provides the most parsimonious explanation. Higher rates of tail-switching in large bovids has apparently selected for the evolution of longer tails that act as more efficient fly swatters. Future studies could further explore the predictions of the peripheral stimulation model by measuring the actual rate of insect attacks on hosts in addition to the rate of insect-repelling movements, or by manipulating attack rate under experimental conditions.

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APPENDIX 1

Mass, morphometric measurements, and typical group size for adult females of selected ungulate species

Species	Common name	Mass*	Shoulder height	Tail length	Head–body	Tail/ body	Tail/ flank	Tail/ shoulder	Group size
Aepyceros melampus rendilis	Kenyan impala	50	86	30	128	0.23	0.44	0.29	58
Antilope cervicapra	Blackbuck	35	72	14	125	0.11	0.65	0.43	36
Bison bonasus bonasus	Lowland wisent	675	188	80	290	0.28	0.81	0.51	11
Bos gaurus gaurus	Indian gaur	825	193	85	275	0.31	0.62	0.49	28
Bos javanicus javanicus	Javan banteng	650	155	68	208	0.33	0.74	0.53	8
Boselaphus tragocamelus	Nilgai	169	135	48	200	0.24	0.24	0.19	14
Capra falconeri heptneri	Turkomen markhor	41	84	11	145	0.08	0.36	0.27	53
Connochaetes taurinus albojubatus	Eastern white-bearded gnu	200	130	80	205	0.39	1.00	0.58	10
Damaliscus dorcas phillipsi	Blesbok	62	93	38	150	0.25	0.89	0.53	9
Damaliscus lunatus jimela	Jimela topi	112	111	39	190	0.21	0.79	0.48	6
Gazella granti roosevelti	Roosevelt's gazelle	51	83	28	103	0.27	0.63	0.38	24
Gazella subgutterosa subgutterosa	Persian goitered gazelle	36	59	15	74	0.20	0.61	0.31	25
Gazella thomsonii thomsonii	Thomson's gazelle	20	59	23	93	0.25	0.22	0.20	24
Hippotragus niger niger	South African sable antelope	210	126	45	210	0.21	0.69	0.45	12
Kobus ellipsiprymnus adolfifriderici	Lake Victoria defassa waterbuck	175	113	29	145	0.20	0.31	0.24	29
Kobus ellipsiprymnus ellipsiprymnus	Ellipsen waterbuck	175	113	29	145	0.20	0.31	0.24	37
Kobus kob thomasi	Uganda kob	64	78	24	138	0.17	0.58	0.39	23
Kobus megaceros	Nile lechwe	75	83	45	135	0.33	0.56	0.44	19
Oryx gazella callotis	Fringe–eared oryx	202	113	68	198	0.34	1.29	0.78	52
Oryx gazella gazella	Gemsbok	202	113	68	198	0.34	1.29	0.78	23
Oryx leucoryx	*Arabian oryx*	155	88	45	132	0.34	0.59	0.41	22
Ovis orientalis gmelini	Armenian mouflon	40	96	11	150	0.07	0.19	0.15	63
Ovis vignei arkal	Transcaspian urial	62	96	11	150	0.07	0.19	0.15	38
Syncerus caffer caffer	Cape buffalo	576	158	93	275	0.34	0.83	0.63	12
Taurotragus oryx pattersonianus	East African eland	450	145	65	240	0.27	1.35	0.66	15
Tragelaphus spekei spekei	East African sitatunga	72	90	24	133	0.18	0.63	0.45	13

*Mass (kg); shoulder height, tail length, and head–body (cm); tail/body ratio = tail length/head–body; tail/flank and tail/shoulder ratios from caliper measurements of photographs, in arbitrary units.

All measurements are taken from Grzimek (1968), Haltenorth & Diller (1980), MacDonald (1984), Gurung & Singh (1996), Kingdon (1997), Nowak (1999).

APPENDIX 2

Mean insect-repelling movements per 3 min for tail switches, ear flicks, head shakes, and foot stamps performed by females of bovid species at San Diego Wild Animal Park during summer 2001

Scientific name	Common name	*N*	Tail switches	Ear flicks	Head shakes	Foot stamps
Aepyceros melampus rendilis	Kenyan impala	9	9.0	3.4	0.3	0.2
Antilope cervicapra	Blackbuck	12	6.9	8.7	0.3	0.6
Bison bonasus bonasus	Lowland wisent	4	178.0	2.5	0.0	0.5
Bos gaurus gaurus	Indian gaur	11	84.8	16.3	0.3	0.1
Bos javanicus javanicu	Javan banteng	6	113.8	9.5	1.0	0.0
Boselaphus tragocamelus	Nilgai	7	22.1	20.9	1.9	0.1
Capra falconeri heptneri	Turkomen markhor	8	4.4	3.2	0.1	0.8
Connochaetes taurinus albojubatus	Eastern white-bearded gnu	4	34.8	40.0	1.0	0.0
Damaliscus dorcas phillipsi	Blesbok	4	11.0	8.1	2.0	1.8
Damaliscus lunatus jimela	Jimela topi	2	16.0	5.5	0.0	0.0
Gazella granti roosevelti	Roosevelt's gazelle	11	86.0	6.9	0.2	0.6
Gazella subgutterosa subgutterosa	Persian goitered gazelle	11	75.1	4.6	0.5	0.5
Gazella thomsonii thomsonii	Thomson's gazelle	10	32.7	0.8	0.1	0.0
Hippotragus niger niger	South African sable antelope	2	95.5	14.5	1.5	3.0
Kobus ellipsiprymnus adolfifriderici	Lake Victoria defassa waterbuck	10	32.9	2.4	1.3	1.1
Kobus ellipsiprymnus ellipsiprymnus	Ellipsen waterbuck	10	47.9	0.6	2.1	0.2
Kobus kob thomasi	Uganda kob	10	109.0	18.8	1.2	0.3
Kobus megaceros	Nile lechwe	9	41.4	37.0	0.2	0.0
Oryx gazelle callotis	Fringe-eared oryx	8	51.1	33.8	0.1	0.0
Oryx gazelle gazella	Gemsbok	7	26.3	8.8	0.4	0.4
Oryx leucoryx	Arabian oryx	10	37.7	20.6	0.7	5.3
Ovis orientalis gmelini	Armenian mouflon	10	5.2	8.5	0.6	0.5
Ovis vignei arkal	Transcaspian urial	3	61.5	1.9	2.1	0.0
Syncerus caffer caffer	Cape buffalo	2	102.0	27.0	1.5	0.5
Taurotragus oryx pattersonianus	East African eland	5	114.8	7.0	0.2	0.0
Tragelaphus spekei spekei	East African sitatunga	7	31.7	5.1	0.1	0.0