



Thermoregulation and Response to Competition in the African Dung Beetle *Kheper nigroaeneus* (Coleoptera: Scarabaeidae)

Author(s): Brent A. Ybarrondo and Bernd Heinrich

Reviewed work(s):

Source: *Physiological Zoology*, Vol. 69, No. 1 (Jan. - Feb., 1996), pp. 35-48

Published by: [The University of Chicago Press](http://www.press.uchicago.edu)

Stable URL: <http://www.jstor.org/stable/30164199>

Accessed: 16/04/2012 04:04

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *Physiological Zoology*.

Thermoregulation and Response to Competition in the African Dung Beetle *Kheper nigroaeneus* (Coleoptera: Scarabaeidae)

Brent A. Ybarrondo^{1,*}

Bernd Heinrich²

¹Department of Biology, Adams State College, Alamosa, Colorado 81102;

²Department of Zoology, University of Vermont, Burlington, Vermont 05405

Accepted 5/1/95

Abstract

Previous studies have shown that some large African dung beetles maintain an elevated thoracic temperature while constructing and rolling dung balls, while others allow body temperature to decline to near ambient temperatures. These studies suggest a causal relationship between elevated thoracic temperature and intense competition for dung. The ability for endogenous temperature regulation is well developed in Kheper nigroaeneus, a diurnal dung ball roller found in Kruger National Park, South Africa. We studied K. nigroaeneus on the dung of large herbivores during the rainy season. We here report that, although winners of conspecific contests for possession of already constructed dung balls have significantly higher thoracic temperatures than losers, K. nigroaeneus does not maintain an elevated body temperature while making or rolling dung balls under competition. Rather, K. nigroaeneus responds to inter- and intraspecific competition by reducing both ball construction time and ball volume prior to initiating ball rolling, thereby reducing potential loss of energetic investment. On arrival at fresh dung, beetles assessed both dung quality and intensity of competition and often rejected dung that had begun to dry or on which many conspecifics were already present. Alternative dung-handling strategies by other species (e.g., pellet sequestering and kleptoparasitism) are discussed.

Introduction

Many large flying insects are endothermic, and thermoregulation is critical to key components of behavior relevant to ecological success (Heinrich 1993). Elevated thoracic temperature is required during all activities involving constant or frequent periods of flight, whereas a lowered thoracic

*To whom correspondence should be addressed.

temperature conserves energy and is advantageous when flight is not necessary (Heinrich 1972). In some species (e.g., *Bombus* sp.) endothermy is related to resource availability (Heinrich 1979). For example, when resources are low, bumblebees forage with a low thoracic temperature because the cost of endothermy exceeds the potential food reward. Thus, the cost of endothermy when not in flight may be prohibitive, given the resources available.

However, elevated thoracic temperature can greatly increase the speed of movement, and an interesting exception to the general trend of endothermy only during flight is found in some African dung beetles (Coleoptera: Scarabaeidae) while competing for dung (Bartholomew and Heinrich 1978). In Tsavo East National Park, Kenya, different species of dung ball rollers appear to have different thermoregulatory strategies while competing for dung (Heinrich and Bartholomew 1979a). One species (*Scarabaeus laevistriatus*) is nocturnal and encounters intense inter- and intraspecific competition at dung piles. Most individuals maintain highly elevated thoracic temperature (ca. 40°C) not only while flying but also while making and rolling dung balls. Elevated thoracic temperature during ball making and ball rolling appears to aid beetles in both scramble and contest competition. In contrast, *Kheper aegyptiorum* is diurnal, encounters low competition at dung piles, and maintains elevated thoracic temperatures only during flight. However, these results did not address the question of whether or not their respective thermoregulatory responses are facultative or species specific. Alternative strategies that may mitigate the effects of inter- and intraspecific competition include working faster (i.e., maintaining an elevated body temperature) or taking less dung (i.e., maintaining a near-normal body temperature).

In Kruger National Park, South Africa, we observed a diurnal dung ball roller of similar body mass ($\bar{X} = 0.222$ g, $N = 17$) as *S. laevistriatus* and *K. aegyptiorum* under conditions of high and low competition in order to determine if endothermy during ball making and ball rolling is a facultative response to competition and whether behavioral strategies are employed to minimize the effects of competition.

Material and Methods

Study Sites

This study was conducted in Kruger National Park during the early rainy season in late December 1993 and early January 1994. The bushveld in the study area consisted of relatively open grassland with varying density of tree cover, primarily *Acacia* spp. and *Marula* sp. We observed *Kheper ni-*

groaeneus on the dung of a variety of large mammals over the approximately 453 km length of the park. However, rainfall pattern was not uniform throughout the park, and there was a great deal of spatial variation in the emergence of vegetation. In some areas, here referred to as “green,” most of the *Acacia* trees were in bloom, whereas within several kilometers, henceforth referred to as “dry,” the trees and shrubs of the bushveld were still without leaves and flowers. Ultimately, we concentrated our study on two sites: (1) a green area near the Albasini ruins located approximately 40 km southwest of Skukuza and (2) a dry area approximately 25 km south of Skukuza near the Stevenson-Hamilton memorial. At the Albasini site we observed low competition, whereas at the Skukuza site we observed high competition where available dung resources were low relative to the number of beetles that had emerged following the onset of the rainy season.

Dung

Dung pellet shape and consistency varies considerably among species and apparently as a function of diet. For example, elephant dung piles typically consist of six to eight massive boluses (vol ca. 4 L/bolus), giraffe dung piles of dozens of loose pellets of relatively uniform size and near-spherical shape approximately 2.3 cm in diameter (vol ca. 6.4 mL/pellet), and impala dung piles of 100 or more uniform pellets (vol ca. 1 mL each), whereas primate dung (e.g., baboon) was typically a single pasty mass. With a dung ball roller, one might expect foraging behavior to vary considerably as a function of type and quality of dung. We first observed the behavior of beetles on the dung of all of the above mammals and then concentrated most aspects of our study on dung-handling behavior as a function of competition at impala (*Aepyceros melampus*) dung piles, on which beetles were most common.

All data were taken on fresh dung unless otherwise indicated. To ensure dung freshness, we observed donor herbivores until fresh dung was dropped. The diameter of dung balls made by beetles was measured to ± 1 mm.

Competition

Kheper nigroaeneus was the largest beetle observed at any dung pile, and intraspecific competition on impala dung piles was defined in terms of the number of these beetles found on them at any one time. In general, we found competition to be difficult to manipulate in the field; although we tried to increase competition by introducing beetles to a dung pile, usually most simply flew off. Therefore, all competition we report refers

to that which occurred naturally or to reduction in competition by batting beetles away that were approaching an impala dung pile. Unless otherwise indicated, “no competition” is defined as a single beetle present and working in isolation at a dung pile, “low competition” as two or three individuals at a dung pile (where beetles were close enough to permit occasional contact either prior to or during ball construction), and “high competition” as 10 or more individuals at a single dung pile. Elephant dung piles are huge in comparison to those of impala, and several beetles working on different parts of the pile would not necessarily have contact with one another.

Thoracic Temperature

Metathoracic temperature (T_{th}) was measured by inserting a 30-gauge hypodermic probe enclosing a 40-gauge copper-constantan hypodermic thermocouple probe ventrally into the center of the metathorax near the hind coxae and thrusting forward into the thoracic mass and read to $\pm 0.1^\circ\text{C}$ with a Bailey BAT-12 digital thermometer. To minimize the effect of solar radiation and high ambient temperature (T_a), all measurements we report refer to overcast days or shade and are restricted to T_a 's of 24° – 30°C . Thoracic temperatures during contests refer to those that occurred naturally in the field; “winners” were those beetles who secured or maintained possession of the dung ball during a challenge from a conspecific. Contests were generally brief (<10 s) and consisted of chases culminating in beetles' attempting to dislodge one another from the dung ball with violent flicks of the pronotal shield and prothoracic legs. Flight temperatures (T_{th} 's) were obtained by knocking incoming beetles to the ground as they approached a dung pile, while warm-up temperatures (T_{th} 's) were taken by swatting beetles to the ground immediately following takeoff. Ambient temperatures were taken at ground level with the same copper-constantan thermocouple probe and read to $\pm 0.1^\circ\text{C}$ with a Bailey BAT-12 digital thermometer.

Body Mass and Dung Ball Diameter

Body and dung pellet weights were measured with a digital top-loading balance to ± 1.0 mg. Ball diameter was measured to ± 1.0 mm. Dung pellet volumes were calculated from measurements of diameter and length. Ball-making durations refer to the time from which the beetle initiated shredding and patting dung until it rolled a dung ball away.

Results

Regional Habitat Variation

At the Skukuza study site, a dry site in the south-central portion of Kruger Park, whenever fresh dung was dropped beetles typically started to arrive within approximately 1 min. The first large beetles to arrive were usually *Kheper nigroaeneus*. While both impala and primate dung occurred at this site, elephant dung was not found during the study period. However, when elephant dung collected the previous day was provided, these beetles were readily attracted. The Skukuza site was considerably drier than the Albasini site; although some *Acacia* had begun to flower, ground vegetation had not or had barely emerged. At the Skukuza site competition at impala dung was generally high.

The Albasini study site was green. Either more or early rains had occurred, and ground vegetation was significantly more lush. In addition to impala and baboons, elephants were present throughout the study period. At this site competition was low to absent on impala dung.

In areas sampled approximately 300 km north of the study sites (e.g., Shingwedzi), the ground vegetation was dense, and the grass was tall and had already set seed. In this region we found no *K. nigroaeneus*, and we observed few dung scarabs of any kind.

Thoracic Temperature Regulation

Neither T_{th} nor the difference between T_{th} and T_a (i.e., $T_{th}-T_a$) differed significantly between flight and warm-up. Similarly, neither T_{th} nor $T_{th}-T_a$ differed significantly from values during walking or dung ball burying (table 1). However, both T_{th} and $T_{th}-T_a$ were significantly greater during warm-up and flight than during walking or burying (Tukey-Kramer Honestly Significant Difference [HSD] test, $P < 0.05$, $N = 52$).

During rolling of balls made of impala dung, neither T_{th} nor $T_{th}-T_a$ of solitary beetles differed from that of the passive partner (the "rider") of a pair rolling together ($N = 62$; table 2), while both values for the active partner of a pair rolling together were significantly greater than those of its rider and of beetles rolling alone (Tukey-Kramer HSD, $P < 0.05$, $N = 62$). Similar results were obtained when the T_{th} and $T_{th}-T_a$ of beetles during ball rolling were compared across dung types (i.e., impala, $N = 62$; elephant, $N = 3$; and primate, $N = 19$); only the temperature (i.e., both T_{th} and $T_{th}-T_a$) of the active partner of beetles rolling together differed significantly from riders or beetles rolling alone (Tukey-Kramer HSD, $P < 0.05$, $N = 84$; fig. 1).

TABLE 1

Thoracic temperature (T_{th}) and temperature regulation ($T_{th} - T_a$) by activity

Activity	<i>N</i>	T_{th} (°C)	$T_{th} - T_a$ (°C)
Flight	14	39.8 (1.3)	17.6 (1.7)
Warm-up	13	39.3 (1.3)	14.6 (1.7)
Walking	18	30.7 (4.8)	6.8 (5.3)
Burying	7	30.3 (4.8)	4.7 (4.9)

Note. Values are presented as mean (SD).

During contests for possession of dung balls, the T_{th} of winners ($\bar{X} = 39.2^\circ \pm 3.5^\circ\text{C}$) was significantly greater than that of losers ($\bar{X} = 36.9^\circ \pm 3.7^\circ\text{C}$; paired *t*-test, $P < 0.01$, $N = 18$).

Finally, during construction of balls on impala dung neither T_{th} nor $T_{th} - T_a$ differed significantly under conditions of competition or no competition. In the same way, no significant difference was found in either T_{th} or $T_{th} - T_a$ during ball construction on elephant dung under conditions of high competition, low competition, or no competition (table 3). Comparison of T_{th} 's during ball construction across dung types and levels of competition showed that both T_{th} and $T_{th} - T_a$ were higher on the dung of both impala and primates than on elephant dung (Tukey-Kramer HSD, $P < 0.05$; table 4).

Dung Ball Volume and Construction Time

Both ball construction time ($N = 40$) and volume of dung balls made by beetles working alone on impala dung ($N = 78$) were significantly greater when there was no competition; under conditions of low and high competition neither construction time nor ball volume differed (Tukey-Kramer HSD, $P < 0.05$; fig. 2). In the same way, across dung types (i.e., elephant, impala, and primate), both ball construction time ($N = 51$) and volume of dung balls ($N = 107$) made by beetles working alone were significantly greater when there was no competition; under conditions of low and high competition neither construction time nor ball volume differed (Tukey-Kramer HSD, $P < 0.05$; fig. 3). Finally, the volume of dung balls made by beetles working in pairs ($N = 5$) on impala and elephant dung was significantly greater than that of balls made by beetles working alone ($N = 90$; Wilcoxon paired-samples test, $P < 0.01$, $N = 95$; fig. 4).

TABLE 2
Thoracic temperature (T_{th}) and temperature regulation ($T_{th} - T_a$) of Kheper nigroaeneus rolling balls of impala dung alone and as active or passive partner of a pair rolling together

	<i>N</i>	T_{th} (°C)	$T_{th} - T_a$ (°C)
Alone	58	33.0 (3.1)	6.5 (4.1)
Passive	13	32.5 (5.4)	5.7 (3.2)
Active	13	38.9* (3.5)	12.1* (3.9)

Note. Values are presented as mean (SD).
 * $P < 0.05$ (Tukey-Kramer HSD).

Dung-Handling Behavior

We observed *K. nigroaeneus* using the dung of all large mammals that we saw (i.e., elephant, giraffe, primate, impala, and wildebeest). However, dung-

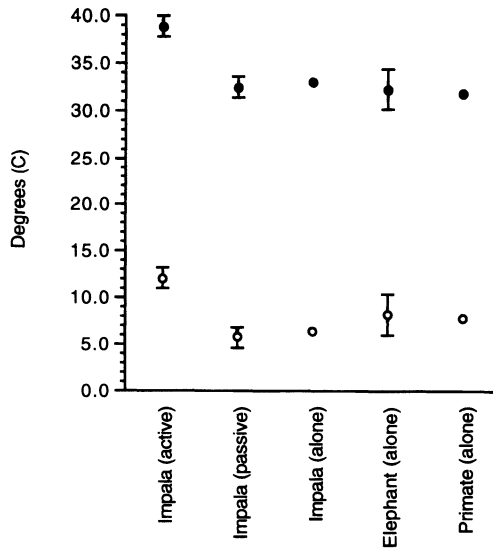


Fig. 1. Thoracic temperatures (filled circles) and temperature regulation ($T_{th} - T_a$; open circles) of *Kheper nigroaeneus* while rolling balls of impala, elephant, and primate dung alone and as active or passive partner of a pair rolling impala dung together. $N = 13$ for impala dung; bars indicate standard errors.

TABLE 3

Thoracic temperature (T_{th}) during ball construction on dung of impala and elephant at various levels of competition

Dung Type	<i>N</i>	Competition	T_{th} (°C)	$T_{th} - T_a$ (°C)
Impala	32	None	33.3 (3.3)	8.0 (3.4)
Impala	35	High	33.8 (4.5)	7.0 (5.0)
Elephant	22	None	28.5 (2.9)	1.9 (2.5)
Elephant	17	Low	28.0 (2.2)	2.9 (2.3)
Elephant	2	High	27.6 (.42)	3.1 (.42)

Note. Values are presented as mean (SD).

handling behavior varied considerably with dung type. Dung-handling time was minimal at giraffe dung; beetles simply rolled individual pellets without modifying their size or shape. In contrast, the much smaller pellets of impala dung were apparently of insufficient size to take individually, and beetles generally shredded one or many pellets with the forelegs and consolidated this material onto a pellet, thereby increasing its size before rolling away a finished ball. With primate dung, the beetles simply carved off a large chunk of the mass and began rolling almost immediately. Finally, on elephant dung, handling time was greatest because, in addition to shredding and adding material to construct a ball, beetles also had to separate the coarsest fibrous material from the dung prior to forming the ball.

TABLE 4

Thoracic temperature (T_{th}) during ball construction across dung types and levels of competition

Dung Type	<i>N</i>	T_{th} (°C)	$T_{th} - T_a$ (°C)
Impala	67	33.5 (3.9)	7.5 (4.3)
Elephant	41	28.3 (2.5)	2.4 (2.4)
Primate	11	33.0 (4.8)	9.0 (4.8)

Note. Values are presented as mean (SD).

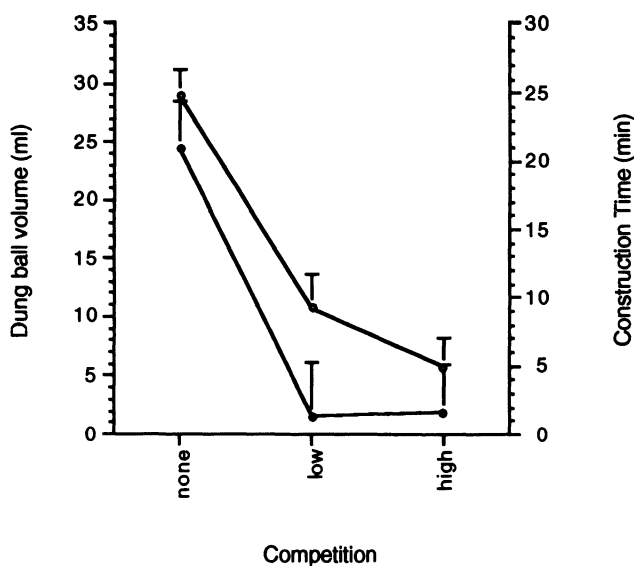


Fig. 2. Dung ball volumes (open circles; $N = 78$) and construction times (filled circles; $N = 40$) for *Kheper nigroaeneus* working alone on impala dung balls under different competition conditions. Bars indicate standard errors.

Impala dung that had been exposed to air for more than 1 h was generally notably dried; following arrival at a dung pile beetles often assessed dung quality and flew off without attempting to construct a ball. Beetles also flew off within seconds of arrival if many conspecifics were already at the dung pile.

Other Behavioral Strategies

A major competitor for dung, *Scarabaeus galenus* (ca. 0.150g), was commonly observed at impala dung piles at some sites. This beetle typically excavated a tunnel on arrival and, normally working in pairs, then proceeded to provision the cavity by carrying individual pellets with the hind legs and dropping them into the hole. When confronting either intra- or interspecific competition, pairs of *S. galenus* would typically divide their efforts, with one beetle defending the tunnel while the other continued to provision the store without interruption. The potential effectiveness of *S. galenus*'s strategy was revealed in one example in which a *K. nigroaeneus* at an impala dung pile had spent 31 min managing to construct a ball consisting of only three pellets. Meanwhile, a pair of *S. galenus* had sequestered 65 pellets from the same dung pile in their burrow located several centimeters from the pile.

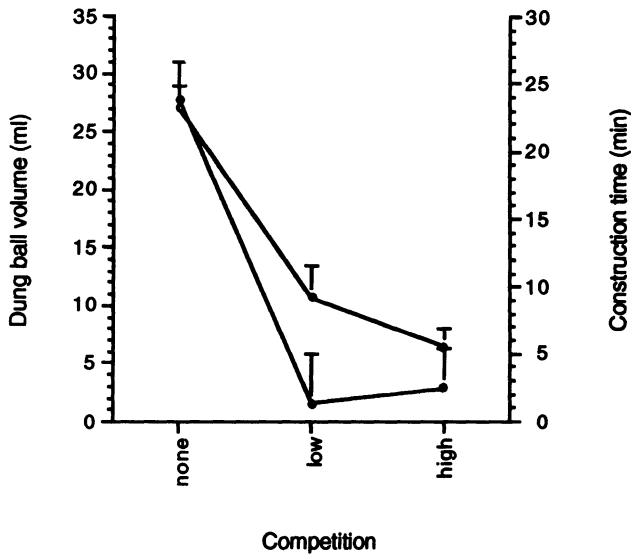


Fig. 3. Dung ball volumes (open circles; $N = 107$) and construction times (filled circles; $N = 51$) for *Kheper nigroaeneus* working alone on elephant and primate dung balls under different competition conditions. Bars indicate standard errors.

Lengthy ball construction is costly in another way. Numerous kleptoparasitic beetles (primarily *Ontophagus* sp. and *Aphodius* sp.) were usually hovering near dung piles and selectively landing on, and instantly burrowing

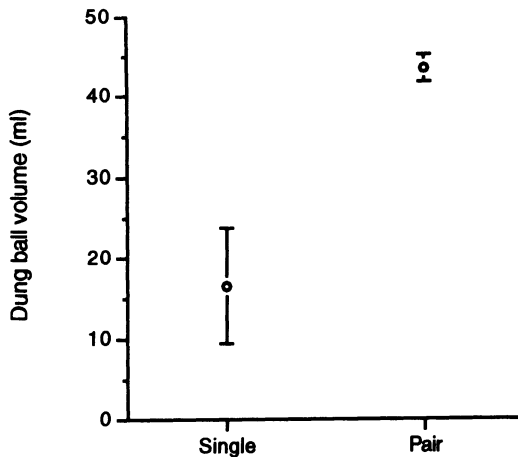


Fig. 4. Dung ball volumes for *Kheper nigroaeneus* working alone ($N = 90$) or in pairs ($N = 5$) on impala and elephant dung balls. Bars indicate standard errors.

into, balls under construction. We dismembered one dung ball constructed by *K. nigroaeneus* (diameter = 3.3 cm) and found 82 tiny kleptoparasitic beetles of three species.

Discussion

Competition among dung beetles at dung piles can be extremely intense and can take the form of both scramble and contest competitions (Heinrich and Bartholomew 1979*b*). Elevated T_{th} has been implicated as an important variable, particularly in nocturnal dung ball rollers experiencing the most intense competition (e.g., *Scarabaeus laevistriatus*; Heinrich and Bartholomew 1979*a*). In contrast, diurnal beetles experiencing low competition (e.g., *Kheper aegyptiorum*) showed little elevation of body temperature. The above findings refer to competition only on elephant dung at Tsavo East National Park. Thus, while these studies revealed interspecific differences in thermoregulatory strategy, they did not establish whether competition or lack thereof affects body temperature.

Body Temperature as a Function of Behavior

In all large endothermic insects, elevation of body temperature results from flight muscle activity (Heinrich 1993). Locating suitable dung often requires flying considerable distances; in addition, beetles must attain a minimum T_{th} before takeoff (Leston, Pringle, and White 1965). Thus, beetles arriving at dung necessarily have an elevated body temperature. Subsequently, however, during walking, ball making, ball rolling, and fighting, an elevated body temperature may be maintained by shivering with the flight muscles (Heinrich 1993), or beetles may cool passively (Bartholomew and Heinrich 1978). During intense competition, *S. laevistriatus* often attempt to steal existing balls from other individuals, and in the ensuing contests beetles having the higher body temperature generally gain possession of the ball (Heinrich and Bartholomew 1979*a*). We here report similar results with *Kheper nigroaeneus*; in contests, winners had on average a T_{th} 2.3°C higher than losers. If a Q_{10} value of approximately 2.0 is assumed, this corresponds to a not insignificant performance advantage of approximately 17%. In the same way, T_{th} during takeoff, flight, walking, ball rolling, and ball riding are comparable to those reported for *S. laevistriatus* (Bartholomew and Heinrich 1978). Beetles working as mated pairs consist of an active ball roller (male) and a passive ball rider (female), who is immobile and clamped onto the ball. During takeoff, flight, and ball rolling, beetles generally maintain a high T_{th} . While walking, T_{th} across beetles is quite variable, which may simply

reflect the amount of time since landing. In contrast to ball rollers, ball riders and beetles burying balls generally maintained low T_{th} 's.

Body Temperature as a Function of Competition

Although *K. nigroaeneus* elevate body temperature by endothermic warm-up as do other large beetles, they apparently do not employ this capability as a strategy in response to competition during ball construction. As during walking, the beetles allowed T_{th} to decline while constructing balls. Since mean T_{th} did not differ across competition conditions and types of dung, we conclude that either beetles do not shiver during ball construction or shivering is not affected by dung type or presence of conspecifics.

Other Strategies for Minimizing the Effects of Competition

According to optimal foraging choice theory, diet breadth increases with decreasing resource availability (Stephens and Krebs 1986). During this study, dung resources appeared to be patchily distributed; therefore, there was generally limited choice in any given area, and *K. nigroaeneus* used whatever dung was available whether no handling time (e.g., giraffe dung) or substantial handling time (e.g., elephant or impala dung) was required in dung ball construction. We concentrated our study on impala dung piles, the most commonly available.

On impala dung, competition had a significant effect on ball construction behavior. Under high levels of competition, beetles spent less than 2 min at a fresh dung pile making small balls (mean vol = 6.9 mL) that were immediately rolled away. This behavior may reflect a strategy of scramble competition. By leaving a dung pile sooner (i.e., with a smaller dung ball), beetles would enjoy several competitive advantages: (1) T_{th} would have declined less; thus, they might still have a chance of winning a contest with a recent arrival and retaining their ball, (2) the number of contests would be greatly reduced, and (3) if a contest were lost, the loss of time and energy invested would be greatly reduced.

Dung Type and Quality

The time required to construct a dung ball varies tremendously as a function of dung type and quality. On some types of dung (e.g., primate dung) beetles can construct a relatively large ball in a short time even under intense competition; thus, although they acquired relatively large dung balls, beetles nevertheless minimized the time spent at the dung pile. In contrast, beetles could generally afford the long handling time required on elephant dung

because competition was low in the Albasini study area. On impala dung, dung quality varied spatially. In some areas having little green vegetation, individual dung pellets were firm and discrete. In other areas having lush vegetation, individual pellets were typically moist and less discrete (i.e., partially compacted). In the former situation, beetles generally accepted dung only for a short period (i.e., <1 h) after it was deposited. Although beetles occasionally attempted to construct a ball from older dung, they experienced difficulty in both shredding pellets and getting processed dung to adhere to the ball under construction. As a consequence, beetles often spent long periods yet constructed small balls, even without competition. Indeed, most beetles inspected and rejected dung piles deposited more than 1 h earlier. In contrast, with moist dung and no competition, beetles spent considerable time making large, firm, well-constructed, and highly spherical balls and never left with small, irregular balls.

Interspecific Interactions

In addition to dung ball rollers who remove dung for use at a location removed from competition, other dung beetles have a variety of strategies for using dung (Heinrich and Bartholomew 1979*b*; Hanski and Combeftor 1991). While some species simply feed on dung in situ, many species burrow directly beneath a dung pile and sequester dung in the burrow to use later in isolation. Our results have suggested some limitations of the ball-rolling strategy on impala dung that derive from the long handling time required for ball making—especially under arid conditions. A strategy observed in *Scarabaeus galenus*, which may be derived from the ball-rolling strategy, is to simply take individual pellets (ca. 1.0×1.2 cm), lift them off the substrate with the hind legs, and, walking backward like a ball roller, deposit them in a nearby burrow that was excavated immediately on arrival at the dung pile. We here show that dung ball rollers respond to competition by making smaller balls; however, below a lower size limit, ball rolling by a large beetle may be less efficient than carrying. Therefore, rather than take the time to shred individual pellets and construct a ball, *S. galenus* simply shuttles between the dung pile and the nearby burrow and deposits pellets. Indeed, we observed this behavior by *S. galenus* at one dung pile where, working under conditions of high competition, a pair of beetles working cooperatively sequestered 65 pellets—far more than the number of pellets incorporated into a ball by a dung roller (ca. three to five) under the same conditions. In addition, this strategy minimizes the effects of both competition and degradation of dung quality due to desiccation. Thus, this may be a strategy derived from that of dung ball rollers (e.g., *K. nigroaeneus*)

that is convergent with that of burrowers (e.g., *Heliocoprus* sp.; Heinrich and Bartholomew 1979b; Hanski and Combefort 1991).

The degradation of dung quality with time is also affected by numerous small beetles that invade dung balls under construction. We routinely observed numerous small kleptoparasitic beetles hovering preferentially around dung balls under construction by *K. nigroaeneus*. This potential "parasite load" presumably further increases the selective pressure for minimizing ball construction time.

Acknowledgments

This study was supported by National Geographic Society grant 4884-92 to B.H. We thank Dr. L. E. O. Braack and Mr. Lynn van Rooyer of the Nasionale Parkeraad (Kruger National Park), Republic of South Africa, for permission and logistical assistance in the conduct of this study. Dr. Henry F. Howden kindly identified the beetles investigated herein. We also thank Beverly and Charles Leach for their kind hospitality while in South Africa.

Literature Cited

- BARTHOLOMEW, G. A., and B. HEINRICH. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. *J. Exp. Biol.* 73:65–83.
- HANSKI, I., and Y. COMBEFORT. 1991. *Dung beetle ecology*. Princeton University Press, Princeton, N.J. 481 pp.
- HEINRICH, B. 1972. Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. *J. Comp. Physiol.* 77:49–64.
- . 1979. *Bumblebee economics*. Harvard University Press, Cambridge, Mass.
- . 1993. *Hot-blooded insects: strategies and mechanisms of thermoregulation*. Harvard University Press, Cambridge, Mass.
- HEINRICH, B., and G. BARTHOLOMEW. 1979a. Roles of endothermy and size in inter- and intraspecific competition for elephant dung in an African dung beetle, *Scarabaeus laevistriatus*. *Physiol. Zool.* 52:484–496.
- . 1979b. The ecology of the African dung beetle. *Sci. Am.* 241:146–156.
- LESTON, D., J. W. S. PRINGLE, and D. C. S. WHITE. 1965. Muscular activity during preparation for flight in a beetle. *J. Exp. Biol.* 42:409–414.
- STEPHENS, D. W., and J. R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, N.J.