Effects of Global Positioning System Collar Weight on Zebra Behavior and Location Error

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ABSTRACT Global Positioning System (GPS) collars are increasingly being used to study fine-scale patterns of animal behavior. Previous studies on GPS collars have tried to determine the causes of location error without attempting to investigate whether the accuracy of fixes provides a correspondingly accurate measure of the animal's natural behavior. When comparing 2 types of GPS collar, we found a significant effect of collar weight and fit on the rate of travel of plains zebra (Equus burchelli antiquorum) females in the Makgadikgadi, Botswana. Although both types of collar were well within accepted norms of collar weight, the slightly heavier collars (0.6 % of total body mass [TBM]) reduced rate of travel by >50% when foraging compared with the collar that was 0.4% of TBM. Collar effect was activity specific, particularly interfering with grazing behavior; the effect was less noticeable when zebras crossed larger interpatch distances. We highlight that small differences in collar weight or fit can affect specific behaviors, limiting the extrapolation of fine-scaled GPS data. This has important implications for wildlife biologists, who hitherto have assumed that collars within accepted weight limits have little or no effect on animal movement parameters.

KEY WORDS behavior, Botswana, *Equus burchelli antiquorum*, Global Positioning System (GPS) collars, location error, zebra.

Over the last decade, the precision and reliability of fix locations provided by Global Positioning System (GPS) collars have enhanced the capacity of wildlife biologists to quantify patterns of behavior, enabling a shift in the focus of telemetry research from simple home range estimation to detailed patch use (Rodgers 2001, Johnson et al. 2002*b*, Adrados et al. 2003, Fortin 2003), estimates of travel speed (Weimerskirch et al. 2002, Nelson et al. 2004), and the breakdown of movement behavior (Moen et al. 1996*a*, Turner et al. 2000, Johnson et al. 2001, Ungar et al. 2005). Radiotelemetry has been used to obtain detailed information on animal ecology (Saunders et al. 1993, White and Harris 1994), but the advent of the GPS collar has enabled researchers to assess these behaviors remotely on far ranging species moving rapidly across inaccessible terrain (Weimerskirch et al. 2002).

In May 2000, the United States Department of Defense deactivated selective availability (Lawler 2000); this reduced the location error of positional fixes that hitherto had limited the efficiency of GPS telemetry without the aid of differential correction (Rempel and Rodgers 1997). Fix precision and accuracy can now be more readily achieved with both differential and nondifferentially corrected collars (Janeau et al. 2001, Adrados et al. 2002), such that it is possible to achieve a positional fix accurate to approximately 3.5–5 m (Janeau et al. 2001, Agouridis et al. 2004) and precise to within 8–12 m (Hulbert and French 2001). However, because variation in precision and location error are still seen to be the most important obstacles in obtaining the desired accuracy required for monitoring animal behavior (Frair et al. 2004, D'eon and Delparte 2005), a great deal of attention has been directed toward trying to eliminate potential bias in GPS telemetry caused by the variation in location error. Causes of location error have been attributed to increasing vegetation height and canopy cover (Rempel et al. 1995, Edenius 1997, Dussault et al. 1999, Frair et al. 2004), the activity patterns of the study animal (Moen et al. 1996*b*, Bowman et al. 2000), and terrain (D'eon et al. 2002). All of these factors affect the ability of GPS collars to locate satellites with which to triangulate their position (Rodgers et al. 1996). Bias in location error and fix rate may therefore be inherent within particular habitat types or during particular behaviors. These issues are of concern to the development and application of GPS technology in animal research, and they must be accounted for in the use and analysis of GPS data. However, very little attention has been focused on trying to determine whether the increasing scale of precision and accuracy obtained by GPS collars portrays a corresponding scale of accuracy and biological relevance to an animal's natural behavior.

The concept that tracking collars have the potential to interfere with the study animal's natural behavior has long been accepted (see Murray and Fuller 2000 for detailed review). The accepted weight ratio of collar to subject depends on the size of the study animal; weights vary from 0.7% to 9% of body mass, with smaller animals generally carrying a greater proportional collar weight (Berteaux et al. 1996, Kumpala et al. 2001). Although <5% of body mass has been suggested as an acceptable standard for the maximum weight of a tracking collar (Macdonald 1978), this paradigm was not based on objective criteria. However, the detailed scale of movement patterns and behavior investigated using GPS collars requires that wildlife biologists also consider the possibility that collar weight and fit may influence data quality (Moen et al. 1996*a*, Johnson et al. 2002*a*, Adrados et al. 2003, Pepin et al. 2004). These factors may be less of an issue when studied at the broader scale of behavior, but as the scale of the

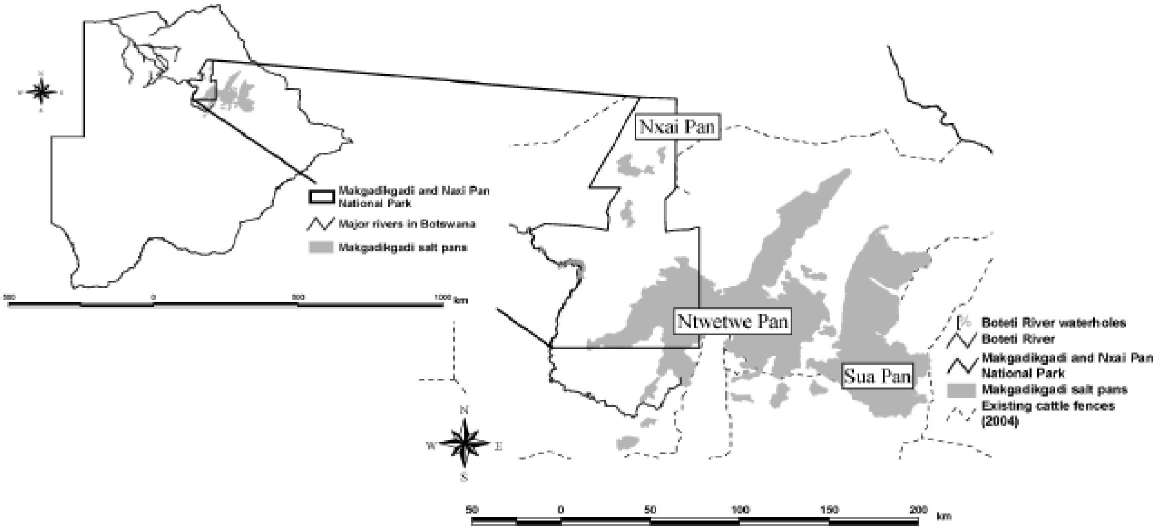

Figure 1. Makgadikgadi and Nxai Pan National Park, Botswana, where we studied the foraging behavior of zebras during 2002–2003 along the Boteti River on the western boundary of the National Park.

investigation is refined the relative effect of collar interference is likely to increase.

As part of a larger study into the ecology of the Makgadikgadi zebra population, Botswana, we investigated the travel speed of plains zebra (*Equus burchelli antiquorum*) within defined categories of behavior using 2 different GPS collars. Our aims were to determine whether differences in collar weight and fit affected the observed rates of travel and whether any variation in observed rate was related to changes in foraging behavior or to specific individual variation among collared zebras. We investigated rates of travel in relation to possible location errors, because differences between the 2 types of collar could have influenced the analysis of travel speed.

STUDY AREA

We conducted our study in the Makgadikgadi and Nxai Pan National Park, between S19°32′–20°50′ and E24°16′–25°07′, in central northern Botswana (Fig. 1). Elevation across the study area was limited, from 910 m in Ntwetwe Pan to the south and east of the National Park to 945 m to the north and west (Grey and Cooke 1977). Tall dense vegetation with closed canopies, which might adversely affect successful GPS location rates, was restricted to a 100–200-m-wide riparian zone following the length of the Boteti River. The riparian vegetation was composed of trees with an average height of 4 m at a density of 28 trees per 100 m^2, and a lower canopy of shrubs with average height 2 m and approximately 900 shrubs per 100 m^2. Zebras drank from waterholes located in the dry riverbed, moving out to graze in open bushveld and savanna grasslands that contained few stands of trees with closed canopies. Average tree density in the open bushveld was 11 trees per 100 m^2, with >1,000 shrubs per 100 m^2, at an average height of 1 m (Kgathi and Kalikawe 1993, Parry 1995, Brooks 2005).

The research occurred during the dry seasons of 2002 and 2003, which in an average year extends from April to October. Rainfall is concentrated within a single wet season, with an average rainfall of 300 mm occurring in the 2001–2002 wet season from November 2001 to March 2002. In the 2002–2003 wet season, there was <200 mm of rainfall, and the dry season extended to December. Resource availability was therefore lower during the 2003 dry season, and the zebras foraged over large areas to find suitable grazing (Brooks 2005).

METHODS

We selected adult zebra females in preference to males to monitor movement behavior to reduce the risk of collar damage during intrasexual fighting. We selected adult females at random from across the population to ensure they were from different harems, and they were darted from a helicopter by an experienced wildlife veterinarian, using the tranquilliser etorphine hydrochloride, M99® (Logos, Avget, Johannesburg, South Africa; Ebedes 1971). Zebras were revived with the antagonist diprenorphine hydrochloride, M50-50® (Logos, Avget; Fuller et al. 2000), and they were active, having safely rejoined their harem, within 25 minutes of the initial darting. Animal handling protocols were approved by the Department of Wildlife and National Parks, Botswana.

During 2003, we used 3 Televilt Posrec™ GPS collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) with 3 D-cell batteries (total wt, 1.2 kg) and 5 Televilt Simplex™ GPS collars with 5 D-cell batteries (total wt, 1.8 kg). Because southern African zebra females weigh approximately 320 kg (Skinner and Smithers 1990), collar weight ratio was approximately 0.4% and 0.6%, respectively; both are at the lower end of collar weight ratios traditionally used in wildlife studies. We designed the Posrec collars especially for zebras to ensure that the satellite antenna was situated vertically at the top of the collar when fitted around the zebra's neck, whereas we adapted the Simplex collars for zebras by reducing the manufactured collar diameter. We placed collars toward the top of the neck with a 2-finger gap between the collar belt and skin. This gap was left to limit any adverse restrictions on the zebra's natural movement and behavior but it was not large enough to allow the collar to slip round the zebra's neck. Adjusting the Simplex collar caused the satellite antenna to sit at 45° from vertical and could have led to a potential bias in location error. This also affected the fit of the Simplex collars; although movement around the anaesthetised zebra's neck was minimal, it was not possible to quantify any possible collar movement after we released the zebras. We programmed both types of collar to record a positional fix on the hour, every hour, 24 hours per day.

To quantify the effects of different foraging behaviors on location error and travel speed, during 2002 we conducted focal and scan observations (Altmann 1974) from sunrise to sunset, 2 days per month for the whole year, for 5 different zebra females fitted with Posrec collars; we compared these observations to GPS movement data from the same period (Brooks 2005). By this means, we identified typical daily behavior (Twine 2002), reflecting large-scale movement patterns over several hours or concentrated spatial foraging behaviors occurring over a period of several days.

We used activity patterns defined in 2002 to categorize zebra activity in 2003, when we defined categories of activity in relation to a central place foraging pattern that all zebra females were observed to follow around the limited water supplies of the Boteti riverbed. Grazing was restricted to relatively small foraging patches (11 ± 8 km^2 [SD]) selected from across the dry season range (1,956 km^2) using an area-restricted search (ARS) strategy (Tinbergen et al. 1967, Benhamou 1992). An ARS is defined by long interpatch movements through areas of poor or less preferred resource availability, interspersed by patches of highly concentrated activity, where the animal intensifies its search strategy to take advantage of localized resources. Zebras walked out from the Boteti waterholes for up to 12 hours in long, straight, and direct paths toward their selected foraging patches. Zebras then spent an average of 3–4 days grazing, foraging, and resting within one defined patch, before returning to the riverbed to drink. Movement rates within the foraging patch therefore include active periods, walking and searching for food, and resting periods with no activity. When leaving a foraging patch, zebras walked directly to waterholes located in a concentrated area of the Boteti riverbed, remaining in the riverbed for approximately 1–2 hours before returning to the same or a new foraging patch (Brooks 2005).

We identified 4 principal categories of activity within the zebra's central place foraging pattern: 1) walking out from the riverbed to the grazing patch, 2) in the foraging patch, 3) walking back to the riverbed from the grazing patch, and 4) in the riverbed. We used the first 3 in the analysis, because time spent within the riverbed was limited, reducing the sample size of fixes within this category. We categorized every positional fix into 1 of these 4 behaviors by analyzing the whole movement path formed by successive fixes. We assessed each fix visually in relation to the previous and subsequent 3 fixes using ArcView 3.2 Geographic Information System (GIS) to detect changes in interfix distance and the angle of travel; a drop in speed and increased tortuosity of movement indicated that the zebra had entered a foraging patch. If the subsequent 3 fixes continued to reflect a change in foraging behavior, we also categorized those fixes within the foraging patch, whereas extensive search behaviors from the riverbed to the grazing patch and back to the riverbed were characterized by long, straight, interfix distances (Benhamou 1992). We preferred a visual analysis of the movement paths rather than categorizing activities by identifying a set change in direction and angle or interfix distance, because a more accurate assessment of spatial variation in movement was possible with visual interpretation of the data.

Within each type of activity we recorded the zebra's rate of travel using ArcView 3.2 GIS and the Animal Movement Extension (Hooge et al. 1999). We estimated movement rates (m/hr) by dividing the total distance travelled within a single activity, measured by interfix distance, by the time taken to travel that distance in hours. Rates of travel recorded while the zebras were in the foraging patch therefore include resting periods, where no movement occurred. This lowers the estimated rate of travel while in the foraging patch as a whole.

When zebras were in the grazing patch, we recorded behaviors such as rolling, which may have affected location error, <1% of the time. Most rest periods occurred while standing, under the shade of an *Acacia* tree if available. This may have affected location error, but tree canopies were not closed and we believed error to be minimal. However, while grazing, the lowered position of the zebra's head altered the angle of the satellite antennae from vertical, possibly affecting location error. When travelling between the grazing patch and the riverbed, zebras walked with their heads up, rarely stopping to rest, graze, or conduct activities that may have contributed to an increase in location error.

We conducted one-way analyses of variance (ANOVAs) to determine differences in fix success rate between collar types and among defined categories of activity. We arcsine transformed percentage 3-dimensional (3D) fix rates before analysis, because these data had a binomial distribution. We used separate Kruskal–Wallis tests to investigate whether there was any difference in the rates of travel observed between individual zebra fitted with either collar type, and we used independent sample *t*-tests to test for differences in the rates of travel recorded by individuals wearing different collars types, overall and within defined behavioral categories. We log transformed rates of travel data before analysis to normalize the data.

RESULTS

GPS Location Error

Fix positions were taken successfully on $99.0 \pm 0.1\%$ (SD) of hourly attempts by Posrec collars and on $95.6 \pm 3.5\%$ by

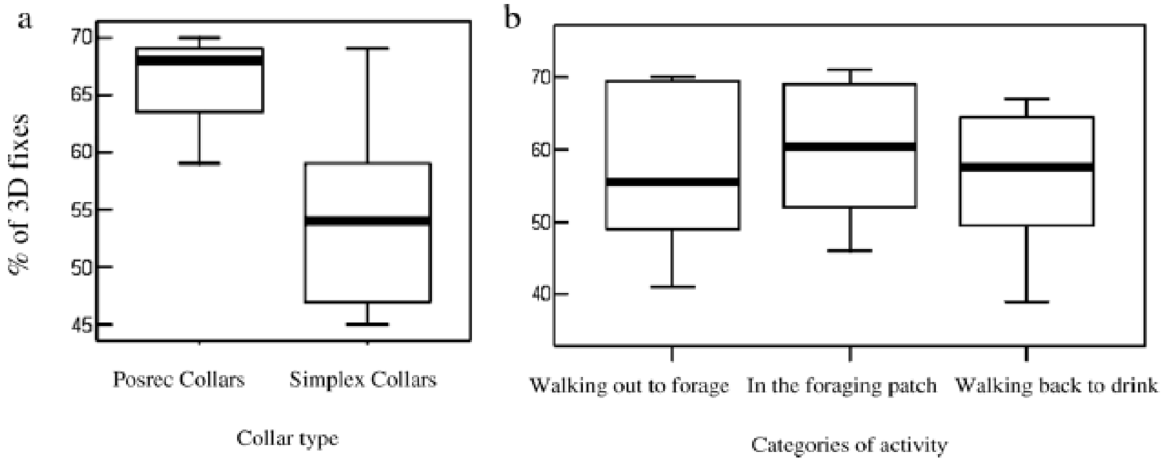

Figure 2. (a) Three-dimensional fix success rate by the different collar types fitted to zebra females in the Makgadikgadi and Nxai Pan National Park, Botswana, during 2003. The box plots display the upper and lower quartile range. (b) Three-dimensional (3D) fix success rate by both collar types across the 3 identified categories of activity identified within the dry season foraging behavior of zebras in the Makgadikgadi and Nxai Pan National Park during 2003.

Simplex collars, giving 34,342 fixes from 8 females ($\bar{x}$ = 4,293 ± 1,032 fixes/F) over the course of the 7-month 2003 dry season. Of these, 65.8 ± 5.49% of the Posrec collar positions were $\geq$3D, indicating that the positional fix was calculated by the triangulation of at least the best 4 visible satellites (Hulbert 2001). Posrec collars had a higher 3D fix rate than Simplex collars (54.8 ± 9.61%) across all 3 categories of activity, but this was not statistically significant (one-way ANOVA: $F_{1,6} = 2.982$, $P = 0.135$; Fig. 2a).

There was no difference in the 3D fix rate taken by both (one-way ANOVA: $F_{2,36} = 0.174$, $P = 0.841$; Fig. 2b) or for either collar type among the 3 categories of activity (one-way ANOVA: Posrec, $F_{2,6} = 0.175$, $P = 0.843$; Simplex, $F_{2,12} = 0.145$, $P = 0.866$).

Rate of Travel Recorded Between Collar Types

The mean dry season travelling speed for all zebras regardless of collar was 0.29 m per second, with a mean rate walking out to the foraging patch of 0.33 m per second, 0.11 m per second within the foraging patch, and 0.42 m per second walking back to the riverbed. There was no difference in observed mean rates of travel among any collared zebra ($P = 0.429$; Table 1). However, there were differences among individuals wearing different collar types for different categories of activity but not among individuals fitted with the same collar type (Kruskal–Wallis: Posrec-collared F: $\chi^2{}_2 = 2$, $P = 0.368$; Simplex-collared F: $\chi^2{}_2 = 4$, $P = 0.406$). Collar effect was activity specific; within the foraging patch zebras with the heavier and worse-fitting Simplex collars travelled at less than half the speed (0.201 ± 0.031 km/hr [SD]) of zebras with the lighter and better fit Posrec collars (0.516 ± 0.005 km/hr; $P < 0.001$; Table 1, Fig. 3). There was also a difference while zebras were walking back to the riverbed to drink ($P = 0.012$; Table 1), but this was proportionally less than that observed while in the foraging patch (Simplex-collared F: 1.416 ± 0.155 km/hr; Posrec-collared F: 1.795 ± 0.124 km/hr).

DISCUSSION

These results were unexpected. Based on accepted paradigms for collar weights, we had assumed that fitting collars that were only 0.4% and 0.6% of total body weight would have no measurable impact on zebra movement patterns. We only discovered that very small differences in collar weight and fit had a significant effect on zebra movements because we used two different types of collar. By using 3 distinct categories of foraging behavior, it was possible to detect a significant effect of collar weight and fit on the zebra's natural behavior that was otherwise masked when rates of travel were analyzed as a mean seasonal rate.

We only investigated 2 different weights and design of collar; testing a yet lighter collar may have shown that Posrec collars also had an impact upon the zebra's natural foraging behavior. Although our results are based on a small sample size and caution must therefore be taken in viewing these results, the substantial difference between the rates of travel recorded by Posrec- and Simplex-collared zebras while they were in the foraging patch gives cause for concern, especially because these collars represent such a small proportion of total body mass. However, our data are comparable with the range of travel speeds recorded for zebras and horses. Walking speed in equids varies between 0.2 m per second and 2.2 m per second (Minetti et al. 1999), with an optimal speed of 0.9–1.25 m per second (Griffin et al. 2000); optimal trotting speeds approximate to 2.7 m per second (Pennycuick 1979).

Observed rates of travel could have been influenced by location error. D'eon and Delparte (2005) have shown that the largest source of location error is collar position and angle, and they recommended that a threshold of 90° from vertical be used to reduce location error. Although adapting the Simplex collars for zebras and adjusting the position of the antennae was within this threshold, collar performance was still reduced and location error increased in comparison with Posrec collars. However, there are 2 reasons why

Table 1. Rates of travel (km/hr) measured by 2 types of Televilt Global Positioning System collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) on free-ranging female zebra in the Makgadikgadi, Botswana, in 2003.

Categories of foraging activity	Mean rate of travel (km/hr)				Test-statistic	P
	Posrec collar		Simplex collar			
	$\bar{x}$	SD	$\bar{x}$	SD		
Total mean rate	1.795	0.124	1.415	0.155	$\chi^2_7 = 7$	0.429
Walking out to the patch	1.285	0.042	1.128	0.221	$t_6 = 1.184$	0.281
In the foraging patch	0.515	0.005	0.201	0.03	$t_6 = 17.116$	≤ 0.001
Walking back to the riverbed	1.795	0.124	1.415	0.155	$t_6 = 3.582$	0.012

location error inherent within the Simplex data cannot explain the difference in rates of travel observed between zebras fitted with different collar types. First, there is no directional bias in GPS location error, and most location error lies within a limit of 100 m, with the majority within 50 m (Moen et al. 1996*b*, Di Orio et al. 2003, D'eon and Delparte 2005). Three-dimensional nondifferential fixes are accurate to within 13 m, whereas 2-dimensional fixes (i.e., calculated using only 3 satellites, which comprised the remaining fixes we used) are accurate to within 28 m (Janeau et al. 2001). Rates of travel recorded by Simplex and Posrec collars differed by >300 m per hour in the grazing patch and by 400 m per hour while walking back to the riverbed to drink. The second reason that inherent location error does not explain the difference in travel rates is that collar effect was activity specific.

Differences in the rates of travel recorded by both collars between categories of activity can be explained by changes in the zebra's foraging strategy. A forager's rate of travel affects its encounter rate with prey (Shipley et al. 1996), and it is directly linked with its optimal energy intake (Murray 1991). Ungulates therefore vary their rate of travel according to the quality of the available sward (Murray 1991). Slower rates of travel indicate the availability of high-quality resources, requiring fewer steps between bites, thereby enabling ungulates to maintain a high instantaneous intake rate (Ungar and Noy-Meir 1988, Murray 1991, Shipley et al. 1996). Faster rates of travel indicate lower-quality resources, forcing ungulates to take more steps between each bite and increasing search rate and frequency of searches between selected grazing sites (Charnov 1976, Bernstein et al. 1991, Shipley et al. 1996). Therefore, following an ARS foraging strategy, we expected the slowest rates of travel while zebras were in their selected foraging patch (Benhamou 1992). The relatively fast rates of travel returning to the riverbed were possibly induced by the zebra's high demands for water after 3–4 days residency within the grazing patch (Brooks 2005). However, we could not link the difference in the rate of travel between collar types while in the foraging patch to variation in individual patch selection and the potential success of each individual to locate a patch of greater quality. We found no relationship between any individual zebra's patch preference or patch selection strategy and collar type (Brooks 2005).

The following questions remain: why was collar effect activity specific and why did it have such a substantial effect on the rate of travel while zebras were in the foraging patch and to a lesser extent while walking back to the riverbed? Although the 600-g difference between collars was slight (approx. 0.2% of body mass), it is possible that this small difference in weight affected foraging behavior by increasing the energetic costs of grazing. Although both collar weights were well within the accepted norms, because an equid's head is 4.5% of total body weight (Sprigings and Leach 1986, Buchner et al. 1997), fitting the collar near the head gives an 8.2% and 12.4% proportional increase in head mass for females wearing Posrec and Simplex collars, respectively. This may have increased foraging costs to the point that Simplex-collared females were compelled to graze on grass tufts closest to their previous bite, rather than raising and lowering their heads to search for tufts of optimal quality.

We fitted all collars to the same standard, with a 2-finger gap between the collar and skin. Although movement of the Simplex collars around the zebra's neck was minimal during fitting, Simplex collars could have slipped forward more than the Posrec collars when the zebra's head was lowered to graze, permitting the collar to rest on the zebra's lower jaw. This would have had a detrimental effect on grazing efficiency, possibly reducing bite rate and rate of movement between sward tufts. However, movement of the Simplex collars was not substantial because we detected no hair loss or sign of skin abrasions around the collars when we removed them. Thus, if Simplex collars had slipped forward more than the Posrec collars, the movement was slight.

Regardless of cause, reducing the rate of travel of Simplex-collared females within the foraging patch to less than half that of the Posrec-collared females would have had a substantial effect upon their ability to maintain minimum daily energy demands, especially in an area of poor resource quality such as the Makgadikgadi (Brooks 2005). By reducing their dependent state, Simplex-collared females may not have been able to increase their rate of travel through the deep Kalahari sands when returning to the riverbed to drink, thereby leading to the slower rates of travel back to the Boteti.

Our results suggest that a significant difference in rate of travel within specific categories of behavior is attributable to differences in collar type. Although further research is required to determine the exact cause of these differences, it

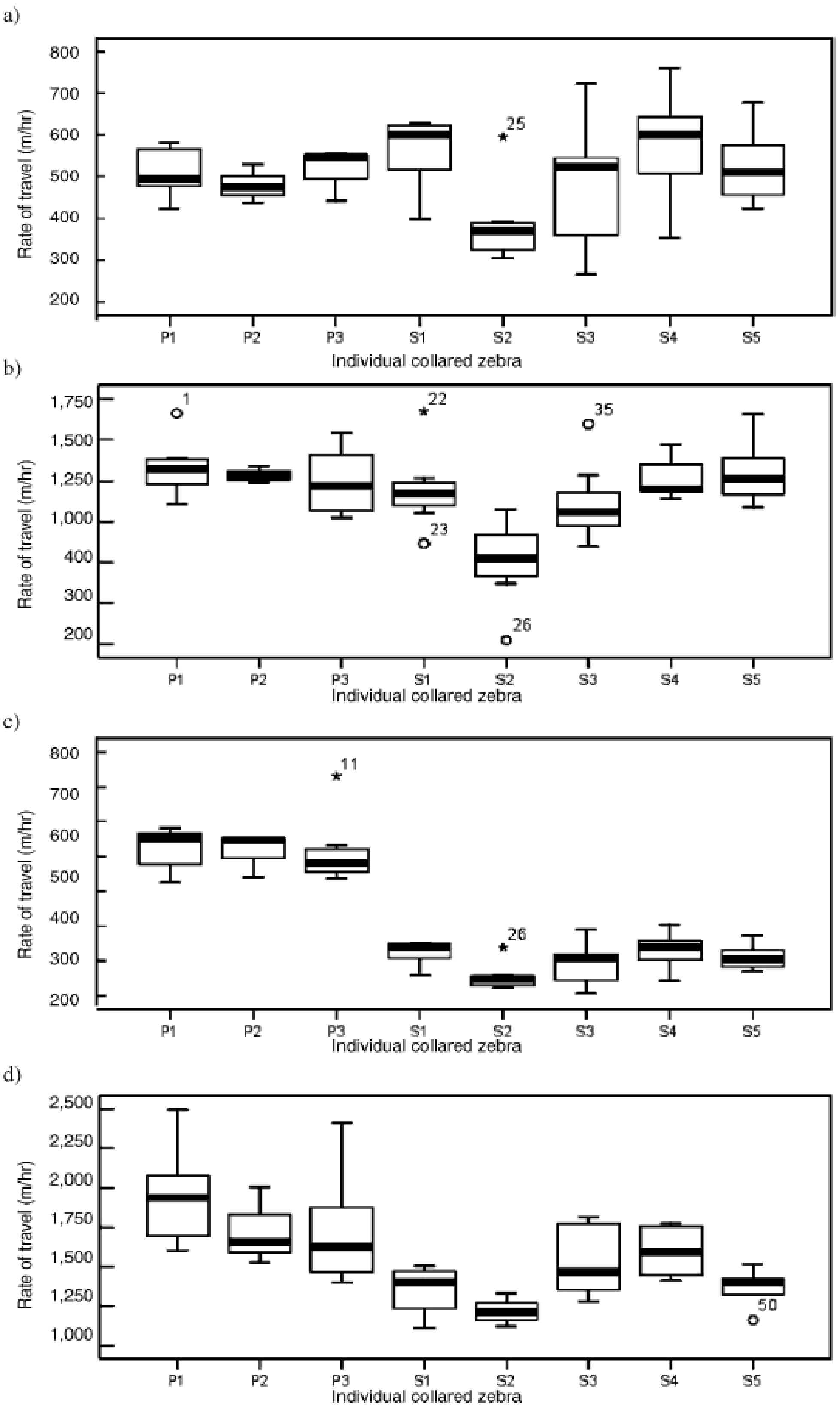

Figure 3. Rates of travel by zebra females throughout the dry season: (a) total mean rate of travel, (b) walking out to the foraging patch, (c) in the foraging patch, (d) walking back to the riverbed. The box plots display the upper and lower quartile ranges of rate of travel, with outliers identified. P1, P2, and P3 denote Posrec collars; S1–S5, simplex collars.

is clear that closer attention needs to be directed at determining animal-specific collar weight, fit, and design standards.

MANAGEMENT IMPLICATIONS

The high degree of location precision, and the large volume of data that can be generated, by modern GPS collars have led to detailed analyses of animal movement patterns, energetics, and fine-scale habitat use. Our experience highlights the need for caution in such studies, because small differences in collar weight can have a significant impact on the measured parameters. It cannot simply be assumed that a collar has no effect on the parameters being measured because it only constitutes a small proportion of total body weight. Location error will continue to decline with improving technology, and the use of GPS collars will become increasingly common in wildlife research (Hulbert 2001, Rodgers 2001). As location error declines and storage capacity and remote relay ability improve, the tendency to refine the scale of investigation will increase. We show that collars with different weights should be compared to see whether there is any detectable impact on the parameters to be measured before the onset of any study using GPS collars.

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