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Microhabitat use and seasonality of the sexually dimorphic West African centaurus beetle *Augosoma centaurus*

Daniele DENDI^{1,2,3}, Stephanie N. AJONG⁴, Edem A. ENIANG⁵, Gabriel Hoinsoudé SEGNIAGBETO^{1,6}, Delagnon ASSO^{1,6}, Guillaume K. KETO¹, Mondjonnesso GOMINA⁷, Raoufou RADJI⁸, Gift Simon DEMAYA⁹, John Sebit BENANSIO⁹, Calogero MUSCARELLA¹⁰, Massimiliano DI VITTORIO¹¹, Julia E. FA^{12,13}, Giovanni AMORI¹⁴ and Luca LUISELLI^{1,2,3}

¹Laboratoire d'Ecologie et Ecotoxicologie, Faculté des Sciences, Université de Lomé, Lomé, Togo, ²Department of Animal and Environmental Biology, Rivers State University of Science and Technology, Port Harcourt, Nigeria, ³Institute for Development, Ecology, Conservation and Cooperation, Rome, Italy, ⁴Department of Fisheries, Lagos State University, Lagos, Nigeria, ⁵Department of Forestry and Wildlife, University of Uyo, Uyo, Nigeria, ⁶Togolese Society for Nature Conservation (AGBO-ZEGUE NGO), Lomé, Togo, ⁷Laboratoire d'Entomologie Appliquée, Faculté des Sciences, Université de Lomé, Lomé, Togo, ⁸Laboratory of Forestry Research, Lomé, Togo, ⁹Department of Wildlife Science, University of Juba, Juba, South Sudan, ¹⁰Cooperativa Silene a.r.l., Palermo, Italy, ¹¹Ecologia Applicata Italia s.r.l., Termini Imerese, Italy, ¹²Department of Natural Sciences, School of Science and the Environment, Manchester Metropolitan University, Manchester, UK, ¹³Center for International Forestry Research (CIFOR), Bogor, Indonesia and ¹⁴National Research Council (C.N.R.), Institute of Research on Terrestrial Ecosystems, Rome, Italy

Abstract

The sexually dimorphic dynastine centaurus beetle, genus *Augosoma* (Coleoptera: Scarabeidae), is endemic to tropical Africa where two species are found (*A. centaurus* and *A. hippocrates*). These beetles are consumed by rural populations, cause damage in plantations and are targets of insect collectors and traders. We present information on size differences and analyzed intersexual niche divergence and seasonality of *A. centaurus* in seven study sites in three West African countries (Ivory Coast, Togo and Nigeria). We recorded 711 light-attracted and/or opportunistically encountered individuals, as well as another 97 beetles in standardized transect surveys. In the latter, we found the adult sex ratio was equal, but was significantly skewed towards females in light-attracted and/or opportunistically encountered individuals. In a sample of 298 adult beetles, males were significantly larger than females, with almost no size overlap between sexes. Beetle activity was highly seasonal with most animals observed in November, active from 19:00 h to 24:00 h. Differences in habitat use were not significant between sexes, with most individuals observed in secondary forest. Males were found higher on vegetation than females and beetles of both sexes were found on *Pandanus* and raffia palms. Beetles were larger in sites with more vegetation cover, and there was a significant effect of tree species on body size of both sexes. Study area or country had no effect on any of the studied parameters. Our study confirms that transect surveys without light trapping can be an effective tool for understanding large-sized tropical beetles of similar ecological characteristics.

Key words: *Augosoma centaurus*, Coleoptera, ecology, Scarabeidae, sexual size dimorphism.

INTRODUCTION

Pronounced sexual dimorphism is often correlated with ecological divergence between sexes in sexually polymorphic species (Houston & Shine 1993; Voight 1995; Walker & Rypstra 2002; Law & Mehta 2018; Li & Kokko 2021). Examples of extreme cases of pronounced sexual dimorphism in size and shape are found in the Dynastinae or rhinoceros beetles, a sub-family of the scarab beetle family Scarabaeidae (e.g., Endrödi 1985; Ratcliffe & Cave 2006, 2015; Ratcliffe *et al.* 2013; Milani 2021). The most striking example is found among the Central American Hercules beetles: in the genus *Dynastes*, males possess long thoracic horns that allow them to reach 173 mm in total length (Keller & Cave 2016). Conversely, females are dull, approximately 55–65 mm long, and without thoracic horns (Keller & Cave 2016).

Extreme sexual dimorphism in dynastine beetles is likely to have evolved for sexual selection reasons (Endrödi 1985), and is correlated with ecological divergence in some scarabeid beetles (Colville *et al.* 2018). However, in dynastine beetles it is unknown whether these significant sex differences in morphology and size are also related to niche divergence in ecological characteristics.

The genus *Augosoma* is the only African representative of the Dynastini tribe and comprises two species endemic to tropical Africa: *Augosoma centaurus* Fabricius, 1775 largely distributed all over the tropical Africa and *Augosoma hippocrates* Milani, 1995 known exclusively for the male holotype collected in Gabon (Muafor *et al.* 2012; Milani 2021). In both species the males, whose dimensions vary from 40 to 90 mm in total length, have blackish brown shiny integuments and are equipped with two exceptionally developed horns: one cephalic, curved and directed backwards,



Figure 1 Male *Augosoma centaurus* from southern Nigeria. Photograph: S.N. Ajong.

up to 30 mm long with an internal protuberance facing the distal part, and the other, thoracic, oriented forward, bifid in its apical part with two lateral outgrowths at the base (Fig. 1). The horns can be extremely small (approximately 4 mm) in smaller individuals. The females of *A. centaurus* (female of *A. hippocrates* is unknown) are similar to the males, except that they have no horns and the length of the anterior tibia is shorter than in the males (Venard-Combes & Mariau 1983; Endrödi 1985; Milani 1995). Centaurus beetles are consumed by rural people in some parts of Africa and therefore represent an important source of protein for these human populations (Muafor *et al.* 2012, 2014; Mabossi-Mobouna & Malaisse 2020). These beetles are of economic relevance due to the damage they can cause in plantations (Guérout 1974; Venard-Combes & Mariau 1983) but are also a target of insect collectors and traders (Muafor *et al.* 2012). Despite this, the ecology of this group of beetles remains little studied, and even less is known about intersexual differences in niche characteristics. Here, we analyze various aspects of the ecology of the centaurus beetle (*A. centaurus*) in seven distinct study sites in three West African countries (Ivory Coast, Togo and Nigeria) and discuss intersexual niche divergence in this species.

MATERIALS AND METHODS

Study areas and sampling

Beetles were studied at two localities in Cote d'Ivoire (San Pedro and Issia), three localities in Togo (Atakpamé, Missahohé and Kpalimé) and two localities in Nigeria (Sagbama and Obudu) (Fig. 2). All these study sites were characterized by a patchy mosaic landscape, including secondary forest, grasslands and plantations and suburban habitats. Plantations were mostly coffee and cacao, pineapple, banana, plantain, oil palm, yam and cassava. The climate of all these study areas was similar, being tropical with a dry season from October to March and a wet season from April to September.

Fieldwork was carried out, at irregular time intervals, during 1992–2021, alongside long-term field research on other organisms, mainly reptiles. We ensured a similar sampling effort each month of the year, undertaken during the same time of the day in all habitats. We sampled beetles 8 days per month in each country (i.e., a total of 24 days per month throughout the study period). During each field day, the study areas were randomly searched from 06:00 to 24:00 h trying to spend, as much as possible, similar amounts

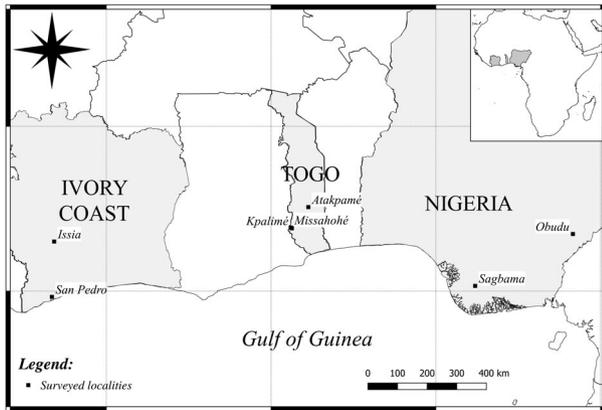


Figure 2 Map of West Africa, showing the various study areas.

of time in each habitat type. Like methods used for monitoring other forest beetle species (e.g., Chiari *et al.* 2013; Bardianni *et al.* 2017) we recorded all adult *A. centaurus* observed along dirt tracks and paths in forested areas (visual encounter surveys). We used an LED headlamp at night. In each study site, transects were walked concurrently by three persons moving independently of each other. We also recorded individuals that were found dead on the ground, or that arrived attracted by light at night, during field days that were not specifically devoted to beetle sampling. However, these opportunistically collected individuals were used only for some types of analyses in this paper (see below for specifications).

For each beetle recorded, we noted sex, date of sighting, time and habitat at the sighting spot. We classified habitats as: (i) mature forest; (ii) secondary forest; (iii) plantation and grassland; and (iv) suburban area. We also measured the total length (mm) of the animals observed, height above ground (cm) if not flying, as well as the tree/plant species on which the beetle was seen perching. We also recorded the diameter at 1 m from the ground of the tree/plant on which the beetle was rested. The following tree diameters were used: 0, on a non-arboreal plant, 1, <10 cm; 2, 10.1–20 cm; 3, 20.1–35 cm; and 4, >35 cm.

Statistical analyses

Artificial-light-trapped beetles (Owens & Lewis 2018) were considered for analyses on monthly and seasonal activity patterns and for sex ratios but were excluded from our habitat analyses. This was because we could not be sure of the microhabitat characteristics used by these specimens, given that: (i) individual insects can travel considerable distances when attracted by

artificial light sources (Degen *et al.* 2016); and (ii) the two sexes can be differently attracted by artificial lights, thus biasing our sex ratio estimates (Altermatt *et al.* 2009; Garris & Snyder 2010; Goretti *et al.* 2011; Singh *et al.* 2014; Chordas & Tumilson 2017).

Daily activity patterns were studied by dividing the period 06:00–24:00 h into four time periods and assigning each beetle recorded to one of these time intervals. The four time periods were as follows: (i) 06:00–09:00 h; (ii) 09:01–12:00 h; (iii) 12:01–18:00 h; and (iv) 18:01–24:00 h.

Observed-*versus*-expected χ^2 -test was used to evaluate: (i) the population sex-ratio; and (ii) the frequencies of individuals of both sexes observed in each month. Intersexual differences in total length were assessed by Student's *t*-test. Generalized linear models (GLM; Hosmer & Lemeshow 2000) were used to test the effect of sex, season (dry *vs.* wet season), country, vegetation cover (defined as the percentage cover of vegetation in a circle plot of approximately 100 m diameter around the sighting spot of the beetle individuals), height from soil, tree size categories, tree species and sighting hour on *A. centaurus* length (mm). The best subset procedure was used. In all models, the identity link function and a normal distribution of error were used (McCullagh & Nelder 1989). We also tested the effect of environmental variables on *A. centaurus* sex using GLM with the logit link function and a binomial distribution of error (McCullagh & Nelder 1989). We selected the best model ranked by the Akaike information criterion corrected for small sample sizes (Akaike 1973, Burnham & Anderson 2002). Alpha was set at 5%, and all tests were carried out using Statistica 6.0 version. Mean is followed by ± 1 SD.

RESULTS

Overall, we recorded a total of 711 light-attracted and/or opportunistically encountered individuals (females, 483; males, 228). We also encountered 97 beetles (females, 47; males, 50) during standardized transect surveys in our study. The adult sex ratio was equal ($\chi^2 = 0.092$, d.f. = 1, $p = 0.760$) in the case of standardized surveys, but significantly skewed towards females if only light-attracted and/or opportunistically encountered individuals were considered ($\chi^2 = 47.216$, d.f. = 1, $p < 0.0001$). The observed sex ratio differed significantly between standardized surveys and opportunistic encounters ($\chi^2 = 14.958$, d.f. = 1, $p < 0.001$). All these data from light traps were pooled as we did not detect any local scale or country effect (see below for statistical specifications).

Overall, we measured total length of 298 adult beetles. Males were larger ($x = 77.6 \pm 7.2$ mm, range = 63.5–95.7 mm, $n = 130$) than females ($x = 57.5 \pm 4.1$ mm, range = 48.1–67.1 mm, $n = 168$); this difference was significant ($t = 30.63$, $p < 0.000001$) and with almost no size overlap between sexes (Fig. 3).

The frequencies of observed individuals differed significantly among months in both males ($\chi^2 = 42.2$, d.f. = 11, $p < 0.0001$) and females ($\chi^2 = 39.8$, d.f. = 11, $p < 0.0001$), with the peak of records in November for both sexes (Fig. 4). Individuals of both sexes clearly showed nocturnal above-ground activity, with the greatest numbers of beetles observed after 19:00 h:

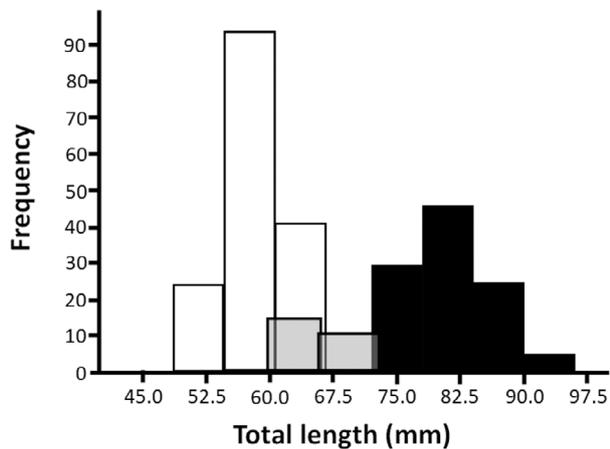


Figure 3 Total length frequency distribution between sexes of *Augosoma centaurus* from all study sites in West Africa. Total sample size: males, 130; females, 168. Black bars, males; gray bars, body size overlap between sexes; white bars, females.

80.9% males and 97.6% of females were observed between 19:00 and 24:00 h (Fig. S1).

There were no significant differences in habitat characteristics in both sexes (χ^2 -test, $p > 0.300$). For all observed beetles during standardized surveys ($n = 97$), use of the four habitat types was significantly different ($\chi^2 = 66.9$, d.f. = 3, $p < 0.0001$): 56.7% of all individuals were observed in secondary forest, 29.9% in plantations, 10.3% in suburban areas and only 3.1% in mature forest. Eleven specimens were found in banana plantations, 9 in cocoa, and 2 in plantain crops.

We also found significant differences between sexes in the heights at which animals were observed. Males were found at an average height of 181.1 ± 18.0 cm from the ground, and females at 277.5 ± 28.0 cm (for the statistical details, see the GLM below). Beetles were observed climbed or perched on several plant species: *Holoptelea grandis* (1 individual), *Lovoa* sp. (1), *Irvingia gabonensis* (1), *Nesogordonia* sp. (1), *Pterocarpus* sp. (1), *Terminalia* sp. (2), *Vernonia* sp. (2), *Raphia* sp. (4), *Triplichiton* sp. (5), and *Pandanus* sp. (9). In many cases we observed beetles while flying or on ground, or perched on grass and bush species that could not be identified (all these cases are excluded from the above counts). In terms of tree size, four individuals were assigned to category 0, 22 to category 1), 43 to category 2, 17 to category 3 and two to category 4, thus showing that these beetles prefer relatively young trees. No difference emerged between sexes in this regard (χ^2 -test, $p > 0.155$).

Our GLM showed a significant effect of sex on the length of this species (males bigger than females), and that individuals tended to be larger in sites with more vegetation cover (Table 1). Our model also revealed that

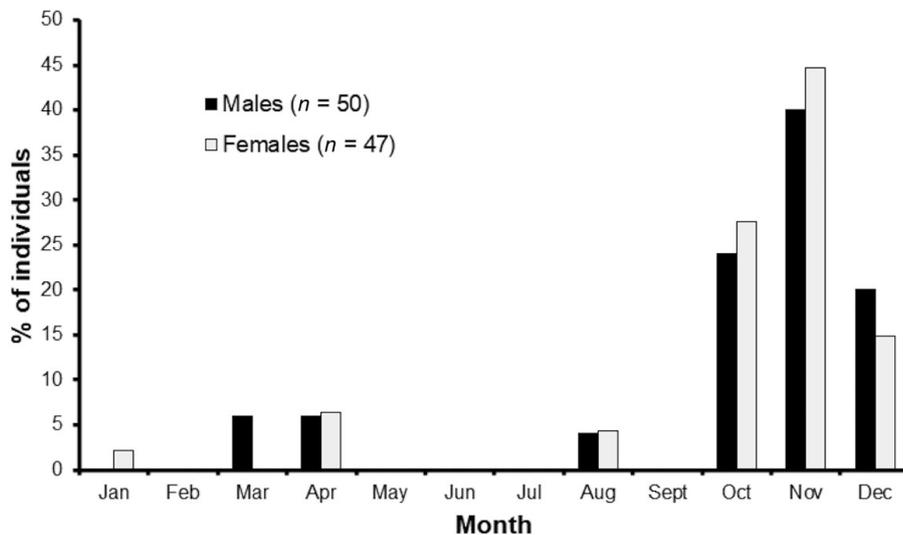


Figure 4 Month-by-month variation in percentage number of sightings of *Augosoma centaurus* individuals of both sexes in all study sites pooled in West Africa. Only beetles encountered during standardized transect surveys are included in this graphic.

Table 1 Results of the generalized linear model on the effects of all covariates on the total length of *Augosoma centaurus* at study areas in West Africa

Covariates	Estimate	SE	Wald	<i>p</i> -value	AICc	d.f.	L. ratio χ^2	<i>p</i> -value
Intercept	121.0595	233.9925	0.267666	0.604	186.12785	3	22.13961	0.000061
Sex	-17.06512	3.95023	18.66264	1.56E-05				
Country	-1.405231	2.387345	0.346469	0.556				
Season	2.3435091	3.172100	0.545807	0.460				
Vegetation cover	11.35654	4.116221	7.611937	0.006				
Height from soil	-1.489824	1.391067	1.14702	0.284				
Tree size category	-4.032600	2.992813	1.815563	0.177				
Tree species	0.924159	0.460483	4.02777	0.044				
Hour	-0.16262	2.473125	0.004324	0.947				
Explained deviance	61.28%							

Note: Bold indicates significance.

Abbreviations: AICc, Akaike information criterion corrected for small sample size; L. ratio, likelihood ratio.

there was a significant effect of tree species on *A. centaurus* body size of both sexes (Table 1). Another model showed that more females than males were significantly more likely to be observed higher on the vegetation (intercept estimate = 1.236, SE = 0.072, Wald = 291.81, $p < 0.0001$; height from soil estimate = 0.0059, SE = 0,001, Wald = 37.91, $p < 0.0001$). Study area or country had no effect on any of the studied parameters (in all cases, at least $p > 0.100$).

DISCUSSION

Our study is one of the first to document some simple ecological features of centaurus beetles in West Africa. As our GLM study did not uncover any local scale or country effect on the investigated parameters, we think that the observed ecological patterns can be generalized for the species across its wide distribution range. An almost equal sex ratio was found in beetles randomly encountered along transects. However, the number of females greatly exceeded that of males for the opportunistically encountered individuals, especially those that were attracted by night lights. Previous studies on conspecifics captured by light trapping at night also revealed a significant female-biased sex ratio (19 374 males *vs.* 46 941 females in the various surveys; see Venard-Combes & Mariau 1983). In another study, the number of males surpassed females in banana plantations in southern Cote d'Ivoire (Guérout 1974). These sex ratio differences could indicate the influence of operational sex ratio (Kvarnemo & Ahnesjo 1996). In *A. centaurus*, where the adult sex ratio is nearly equal, females are much more attracted by light than males, thus explaining the highly biased sex ratio observed in the Cote d'Ivoire study and in our surveys. In contrast, in South American dynastines (genus *Cyclocephala*), females frequently exceeded males (Albuquerque *et al.* 2016). The fact that

one sex was more attracted to light traps is not surprising as it has been observed in other insects (Altermatt *et al.* 2009; Garris & Snyder 2010), but there is considerable variation by species and by localities. For instance, in our unpublished observations from other species, we documented that males are much more attracted to light sources than females in the Sicilian endemic beetle (*Polyphylla ragusae*) (C. Muscarella, 2010-2021, unpubl. data), but much less than the females in the Mediterranean dynastine *Phyllognathus excavatus* (L. Luiselli *et al.*, 2021, unpubl. data).

We found that both sexes are more easily encountered during the early hours of the night, as previously observed in conspecifics from Cote d'Ivoire (Venard-Combes & Mariau 1983). These observations are unsurprising given this is the typical activity pattern of dynastine beetles (Albuquerque *et al.* 2016).

In our study, we showed that *A. centaurus* were active throughout the year but more so during the early dry season (November and December). Previous studies have also indicated that this species is active during this period of the year. Muafor *et al.* (2014) has reported that these beetles are an important protein source for rural communities in Cameroon during the dry season, when bushmeat and even fish are less available. Moreover, Guérout (1974) also reported November as the peak activity month for *A. centaurus* in banana plantations of southern Cote d'Ivoire. The seasonal activity patterns of this species in our study mirror previous studies in other African countries. South American dynastines also show adult activity peak during the dry season (Albuquerque *et al.* 2016).

Interestingly, we revealed that our study species is a habitat generalist (occurring in secondary forests as well as in plantations and in suburbia) but is also selective at the microhabitat scale, given that it was frequently found on plants such as *Pandanus* and raffia

palms that are not the most abundant plant species in their habitat. These plants are often found near marshlands and ponds, thus suggesting that swamp habitats are important for this species across its range. Although no published data are available on *A. centaurus* habitat use, Guérout (1974) also considered that raffia palms were important plant species for this dynastine beetle. In addition, we found that body size was affected by habitat type: vegetation cover increases positively influenced adult male size. The adult body size of Dynastinae is mainly determined by larval nutritional conditions (Iguchi 1998; Keller & Cave 2016). Larvae might obtain lower quality food in the area with lower vegetation cover; thus the positive relationship between vegetation cover and body size is likely due to suboptimal larval diet in altered habitats with low productivity. Our study suggests that mature forests should house larger *Augosoma* beetles than plantations and secondary forests.

Sexual size dimorphism is often accompanied by intersexual differences in niche characteristics (e.g., see Teder & Tammaru 2005; Stillwell & Fox 2007; Law & Mehta 2018; Li & Kokko 2021). As shown in our study, *A. centaurus* exhibits significant sexual size dimorphism where males are considerably larger than females and possess massive head horns (Endrödi 1985). Despite such noteworthy sexual differences in size and morphology the two sexes were found in analogous habitats and showed similar activity patterns (both daily and seasonal). However, we showed that the females tended to perch at higher heights from the soil than the males. Although we do not have data to explain why, we are led to think that this is for antipredator reasons, given that we observed females in four occasions ovipositing on wet soil, thus unlikely to select tree trunks for laying eggs.

Finally, our study revealed that *A. centaurus* can be studied quite easily using appropriate transect surveys and does not require light trapping. We anticipate that the same could be true for other large-sized dynastine beetles that are probably similar in terms of ecological characteristics including, for instance, the South American *Dynastes* and *Megasoma* species. Transect surveys appeared to be very suitable monitoring methods for studying other forest beetles, such as the European *Lucanus*, *Osmoderma* and *Cerambyx* species (Chiari *et al.* 2013) but have not often been applied in tropical species.

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SUPPORTING INFORMATION

Figure S1. Variation in the number of sightings of *Augosoma centaurus* individuals of both sexes by daily time periods. Data from all study sites are pooled for this graph, and only beetles encountered during standardized transect surveys are included. For statistical details, see text.