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Zebra stripes, the ectoparasite hypothesis: using behavioural measures to determine ectoparasitic burdens in plains zebra (*Equus quagga burchelli*) in Addo Elephant National Park, South Africa.

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Zebra stripes, the ectoparasite hypothesis: using behavioural measures to determine ectoparasitic burdens in plains zebra (*Equus quagga burchelli*) in Addo Elephant National Park, South Africa.

William Morgan Connock

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1.0 Abstract.

The drivers behind the unique colouration of the pelage in the three extant species of zebra is a much studied but unsolved question in evolutionary biology. This study aimed to test the ectoparasite hypothesis, which suggests that striping in the pelage of zebras is an evolutionary response to ectoparasitic burdens, specifically biting flies, because the vision system of biting flies is inhibited by such stripes. A population of plains zebra (*Equus quagga burchelli*) in Addo Elephant National Park, in the Eastern Cape province of South Africa were the focus of this study. This population is unique in its reintroductions from a selective breeding program for the near stripeless quagga phenotype creating a large variation in the degree of striping in Addo's zebras. Behavioural observations were employed as a proxy of the ectoparasitic burdens on each animal, a method previously used in the study of plains zebra and other equids. These observations were combined with environmental data and detailed stripe counts for each individual. Whilst stripe counts did not predict comfort behaviour (behaviours associated with the removal or deterrence of ectoparasites), environmental variables, like wind speed, temperature, and humidity, did. This result suggests that previous research citing behavioural intensity as a proxy for ectoparasite loads may require further support from robust invertebrate sampling coinciding with the collection of behavioural data.

2.0 Literature Review

2.1 Introduction

This review of the current literature begins with an introduction to the study of colouration in animals, progressing to a more detailed look at research into striping in zebra. The most popular hypotheses for the role of stripes in zebra pelage will be discussed, examining the theories and the methods used to test them up to this point. The aim is to provide a detailed background of the field whilst also highlighting areas where a greater understanding could be gained.

2.1.1 The study of animal colouration

The study of colouration in animals has long attracted attention particularly since its popularization in the time of Darwin and Wallace. Colouration has been studied in species across the animal kingdom and has been shown to be important in a range of mechanisms such as survival and sexual selection in birds and mammals (Caro et al., 2005, McGraw et al., 2003). Cuthill et al. (2017) compiled a structured approach to explaining the development and purposes of colouration, describing the structural history and formation of colouration through pigments and areas of the body of appendages as well as the ways in which they are utilised. Throughout the long history the ease of measure of colouration and its unfixed nature within and between individuals and populations has lent itself to study. More recently the scope of its study has spread from its evolutionary base to encompass behaviour, perception, and genetics becoming a truly interdisciplinary field.

There are numerous examples of the different uses of colouration in the animal kingdom across taxa, for example in birds, colouration is often employed as a sexual signal in mate selection whether through symmetry (Swaddle and Cuthill, 1994), or quality of pigmentation (Price, 1996), with comparable results being shown in fish (Seehausen and van Alphen, 1998). Colouration can also provide concealment through crypsis to reduce predation risk such as seen in wading bird species at every developmental stage from egg to adulthood (Brown and Shepherd, 1992; Gómez et al., 2015). Opposing this, the same strategies are employed by predators including tiger (*Panther tigris*) and leopard (*Panther pardus*) (Godfrey et al., 1987; Stankowich and Goss, 2006), the great white shark (*Carcharodon carcharias*) (Robbins, 2007), and in cephalopods (*Cephalopoda sp.*) (Hanlon, 2007; Hanlon et al, 2009) as well as in tiger beetle species (*Cicindelinae sp.*) (Schultz and Bernard, 1989), and in the Chamaeleon (*Chamaeleo sp.*) (Cuedrado et al., 2001) to improve hunting success. Many species of insects and reptiles employ colouration to indicate danger or toxicity (aposematosis) (Mappes et al., 2005).

With these cross-taxa commonalities in the use of colouration of varying intensities it is logical to conclude that the more striking an animals' colouration, the stronger its functional role. It is therefore surprising that, in the case of the zebra and its striking pelage, there is not a suitable amount of evidence to determine a functional role, particularly considering their prominence in popular culture and the attention they receive within the academic community. Many of the current hypotheses and conclusions are drawn from research on other species, often taxonomically distant from zebra.

2.1.2 The popular hypotheses for stripes

The role of striping has attracted significant interest over the years with a multitude of published research on the topic (Caro, 2016). Of all the hypotheses considered, the four most supported suggest that the zebra's stripes are an evolutionary response to either predation; social or sexual selection; thermoregulation; or ectoparasitic burdens. Whilst each of these hypotheses has received attention both individually and in comparative studies, none have strong enough support to be considered solely responsible (Gosling, 2017). The ectoparasite hypothesis is the area of research with the most support to date. The basis of this hypothesis is that surfaces with greater intensities of striping experienced reduced ectoparasite landings (Brady, 1972; Davies, 1972; Gatehouse and Lewis, 1973; Vale, 1974; Burgess et al., 1979), with additional evidence showing that horizontally striped surfaces received less landings than vertically striped ones (Waage, 1981; Gibson, 1992). Caro et al., 2019 showed in greater detail how striping effects biting fly landing success. However, due to a lack of conclusive support for this hypothesis recent research has tended towards considering a multi-hypothesis explanation where striping is thought to provide a range of benefits that provide a net advantage (Larison et al., 2015). Additionally, several hypotheses have been dismissed due to lack of evidence or theoretical grounding, such as those considering striping as aposematic colouration (Caro, 2016).

2.2 Predation risk and Camouflage

Historically one of the most popular hypotheses is that striping plays an important role in reducing the risk of predation. To understand this, it is imperative to consider how great the risk of predation is, as it would need to be substantial to drive morphological change over successive generations. Whilst, zebra populations are less vulnerable to limitation by bottom-up processes than other sympatric large ungulates, at a population level, due to their use of the landscape with small familial groups dispersing throughout large areas (Grange and Duncan, 2006). This distribution throughout the landscape reduces the impacts of bottom-up pressures such as localised resource shortages through the populations ability to redistribute (Grange and Duncan, 2006). This large spatial footprint does however lead to a greater chance of members of a zebra population encountering predators (Grange et al, 2004) making them more vulnerable to top-down pressures, such as predation (Grange et al, 2015). This population level vulnerability to predation is further enhanced by aspects of their life history such as the year-round presence of young offspring, increasing sensitivity to predation when compared to the synchronized breeding strategies of large herds of Cape buffalo (*Syncerus caffer*) and blue wildebeest (*Connochaetes taurinus*) (Hillman, 1987; Grange et al, 2004; Grange and Duncan, 2006). Additionally, despite possessing a powerful kick and bite, zebra lack the protection of the goring horns of other species, such as buffalo and sable antelope (*Hippotragus niger*).

The strategy of plains zebra to live in groups reduces the risk of predation through collective vigilance (Pulliam, 1973; Elgar, 1989), in addition to the dilution and confusion effects where increases in prey group size contribute to a reduced chance of an individual being targeted and a lower success rate of predator attacks respectively (Klingel, 1965; Jeschke and Tollrian, 2007; Hamilton, 1971). However, their distinct patterning may make them more

conspicuous than other prey species, potentially leading to a population scale oddity effect making them more likely to be targeted by predators (Hobson, 1968; Landeau and Terborgh, 1986), with group living further increasing visibility to predators compared to lone individuals (Krause and Godin, 1995).

Although the increased protection offered by these groups may reduce predation risk compared to a different strategy, zebra are a preferred prey of the African lion (*Panthera leo*) (Hayward and Kerley, 2005; Lehmann et al., 2008). As with other group living large herbivores, predation risk is clearly substantial as it influences zebra ecology and determines foraging behaviour, causing them to avoid areas of better-quality forage in favour of sub-optimal habitat that has a lower predator concentration (Gakahu, 1982; Fischhoff et al., 2007). Proximity to lions increases herd vigilance leading to reduced foraging rates (Périquet et al., 2012) - further highlighting the pressure imposed by predators through the perception of this risk.

It has been suggested that the zebra's stripes somehow impede predators by conferring confusing visual cues allowing the zebra to evade capture during the initial stages of a chase, and, while only fractionally faster than lion, they are able to outlast the predators' greater initial acceleration (Elliott et al., 1977). Studies have investigated different types of camouflage such as background matching (Kingdon, 1984) and dazzling (Morris, 1990; How and Zanker, 2014).

2.2.1 Background matching

Caro (2005) states "Camouflage appears to be the single most important evolutionary force" in the colouration of mammalian pelage in species other than zebra. If this were the case in zebra there would likely be strong evidence for striping as camouflage through processes such as background matching. This considers that, despite the striking visual impact of a zebra's pelage, stripes afford camouflage against its backdrop. Much of the work in this area suggests that striping may provide some protection from predators through camouflage, but only in specific circumstances (Caro, 2016). The work of Kingdon (1984) suggested that the arrangement of striping affords some camouflage when viewed against habitats in which zebra may be found, such as scrub and tall grass. Although Godfrey et al. (1987) later showed that zebras are not often found in these areas suggesting that such benefits are reduced. Zebra, instead, often forage in open areas, particularly at times when lions are also most active - creating a temporal and spatial overlap in the use of these areas increasing the chance of interactions between predator and prey (Fischhoff et al., 2007, Hayward et al., 2011). Indeed Morris (1990) and later Melin et al. (2016) observed that they seem obvious compared to other sympatric prey species. Additionally, their predator avoidance behaviours are not consistent with a species relying on background matching neither freezing nor attempting concealment when in danger (Kingdon, 1984), but rather moving at speed and turning sharply to escape (Fischhoff et al., 2007). Although research has not provided enough evidence to discount this hypothesis, sympatric mammalian species and indeed other mammals further afield feature much duller pelage patterns in comparison to zebra, which is often thought to be effective camouflage (Caro, 2005) making zebra appear aberrant in terms of camouflage.

2.2.2 Dazzle camouflage

The suggestion that stripes act as a form of dazzle camouflage has also been investigated. This proposes that stripes cause visual confusion in predators causing them to miscalculate attacks. This is thought to be particularly effective when zebra flee predators at high speed when in proximity, where the juxtaposed movement of stripes on the legs and body reduce a predator's ability to predict the location of their prey. This is believed to happen in one of several ways. Firstly, the movement of stripes may generate an illusion of movement, much like the rotation of a barber's pole or the spokes of a wheel spinning at a high rate (Larison et al., 2015), which reduces the success rate of predatory attacks. Morris (1990) suggested that this may therefore be enough to disorientate a predator. Alternatively, it might be that the overlapping broken silhouettes of multiple individuals moving in different direction in a group amplify the confusion effect, reducing a predator's ability to hunt successfully (Eltringham, 1979; Landeau and Terborgh, 1986) due to the exploitation of perceptual bottlenecks (Krakauer, 1995). However, these studies are largely theoretical and there is little empirical evidence to support them. Although Hayward and Kerley (2005) do show that zebra are a preferred prey species of lion, they are not disproportionately hunted above other species that do not feature pelage striping, such as buffalo, gemsbok (*Oryx gazelle*), and blue wildebeest (*C. taurinus*). It may be the case that in the absence of striping predation levels would be higher. However, as Ruxton (2002) suggests, despite the lack of empirical evidence to support this hypothesis, it is not impossible to design a controlled experiment using captive felines and moving striped targets to test this.

2.2.3 Vision in predators

When considering the effectiveness of visual cues, it is important to evaluate the mechanisms by which predators perceive their prey. The works of Kiltie (2000) suggest that visual acuity in large mammalian predators, such as lion, is enough to detect zebra in even sub-optimal conditions. This is further supported by the similar observations of Schaller (1972) and Elliot et al. (1977). This is due to the lions' inability to distinguish stripes in low-light meaning zebra present a uniformly toned silhouette in conditions under which they are most often hunted (Fischhoff et al., 2007), meaning that any visual advantage afforded by contrasting stripes is completely negated in low-light. Furthermore, Kruuk (1972) showed the same for spotted hyena (*Crocuta crocuta*) another potential predator. Additionally, the evidence that zebra are a preferred prey species of lion (Hayward and Kerley, 2005; Lehmann et al., 2008) shows that predation risk is still high.

2.3 Social interaction and hierarchy

The social hypotheses comprise those which consider group cohesion, social hierarchy, and sexual selection. Whilst mate selection has been shown in mammals of both sexes (Orlans, 1969; Stockley and Bro-Jørgensen, 2011), there are few examples of selection based on colouration.

Support for this hypothesis is found in research illustrating the zebra's complex social systems (Klingel, 1965; Joubert, 1972; Chaudhuri and Ginsberg, 1990), to which it could be argued that intraspecific recognition through visual cues is important in zebra (Mills and

McDonnel, 2005). Though these similar hierarchies are present in other wild equids species that do not possess such strong colouration (both the African and Asiatic wild asses (*Equus africanus* and *Equus hemionus*) (Klingel, 1998). Furthermore, it has not been shown whether striping is a factor that dictates an individual's perceived social standing with conspecifics although Caro (2008) suggests that the colouration of zebra could likely be important in conspecific signalling due in part to its individuality.

In mate selection, zebra adhere to the suggestion by Clutton-Brock (2009) that males compete for mates whereas females compete more heavily for the resources that facilitate successful reproduction, primarily territory. It may be that an individual's position in the group hierarchy, or their chance at reproduction, are not directly linked to stripiness (as is commonly thought) but rather to the morphology of their stripes. For this to be consistent with indicating genetic fitness, it would rely heavily upon the strength of pelage pattern heritability. Evidence in this area is sparse, despite the work of Parsons et al. (2007) that demonstrates the strong heritability of stripe number in pelage and the successful selective breeding program of the Quagga project (Harley, 2009), the direct heritability of stripe morphology and shape is yet unproven. Though the field identification system developed by Peterson (1972) which relies on re-occurring pelage formations across a population suggests that the initially seemingly incoherent pattern of striping is more fixed and meaningful than otherwise thought providing a strong basis for a database of stripe morphology in order to investigate heritability.

2.3.1 Recognition in equids

Equids are capable of recognizing conspecifics through olfactory (Feist and McCullough, 1976; Klingel, 1998; Krueger and Flauger, 2011), acoustic (Kiley, 1972; Tyler 1972; Moehlman, 1974; Feist and McCullough, 1976; Moehlman, 1998), and visual cues (Mills and McDonnel, 2005). This suggests that pelage patterns may be at least part of the recognition process between individual zebras and therefore play a role in decisions on fitness in mate selection or hierarchical positioning. That stripes do not play an absolute role in the identification of conspecifics suggests that it is not likely to be the primary function of striping, although this may have contributed to the presence of stripes.

2.4 The thermoregulation hypothesis

The thermoregulation hypothesis is divided into two mechanisms both of which rely on the understanding that zebras experience extremes of temperature (Joubert, 1972). In near equatorial and semi-arid environments, thermoregulation is a key aspect of an animals' fitness especially in quadrupeds due to their horizontal forms absorbing a higher amount of solar radiation than bipeds (Wheeler, 1991). The simpler of the two hypotheses is that striped pelage allows for a dispersal of pigmentation throughout the body that leads to an advantageous balance between cooling during the hottest parts of the day and retaining heat during the coldest parts of the night through the better reflection of heat away from areas of dense vascularity during period of high temperature when cooling is imperative and retention of heat in areas that are less vascular and therefore less able to adapt blood flow to temperature change through vasodilation and vasoconstriction (Kingdon, 1984).

The more complex theory is that the contrast between the black and white areas of their pelage create micro-currents in the air over the surface of the pelage creating an insulating layer of air that protects the zebra from extremes in temperature (Morris, 1990). These hypotheses therefore imply that this selection pressure would not be present in sections of the species' range where potentially high temperatures are dissipated by wind - conditions which would also disrupt insulating micro-currents. The work of Hiley (1977) shows that zebra's initial physiological response to a raised body temperature is an increased rate of respiration, which is a key mechanism for cooling in mammals (Richards, 1968), rather than increased perspiration which is seen in sympatric rhinoceros species (*Diceros bicornis* and *Ceratotherium simum*). This difference may simply be down to the comparative lack of hair, or it may be that the pelage of zebra, in combination with respiration provides a more efficient method of thermoregulation. Further weight for these hypotheses is provided by Larison et al. (2015) who modelled striping in several equid species against a range of biotic and abiotic factors across a large spatial scale and showed that only temperature was a strong predictor of striping. However, this also provides support for the next hypothesis to be presented, ectoparasite burdens, as many of the biting fly species that feed on zebra are associated with high temperatures (Herczeg et al., 2015).

2.5 The ectoparasite hypothesis

One of the most supported hypotheses concerns ectoparasites - first raised in the early twentieth century by Harris (1930) - and suggests that striping has a negative effect on the ectoparasitic loads of zebra. The evolutionary basis of this is that parasite burdens can incur multiple fitness costs including: severe blood loss (Steelman, 1976); reduced foraging due to irritation (Hunter and Moorhouse, 1976; Harris et al., 1987; Lehane, 2005); or disease transmission including sleeping sickness and blood parasites including trypanosomes (McCulluch, 1967; Foil, 1989; Hall et al., 1998; Moehlman, 2016). To further support this idea, it has been shown that parasitic burdens have impacted the evolution of sexual signals and colouration in other animals. For example, Hamilton and Zuk (1982) showed that blood parasites reduced the quality of sexual signals in passerines leading to mate selection based on signals that indicated a stronger genetic resistance to parasitic burdens. Andersson (1994) expanded on this, going on to detail the relationship between the strength of sexual signal and genetic fitness. This area of study has support from both lab and field-based work that has shown reduced attraction to striped surfaces in the *Glossinidae* (Tsetse) and *Tabanidae* (Horse flies) families of biting flies (Waage, 1981; Egri et al., 2012; Blahó et al., 2013). Both species are well documented parasites of the plains zebra (Waage, 1981; Egri et al., 2012; Blahó et al., 2013), as well as sympatric equid species (Horak et al., 1986) and other more distantly related ungulates and domestic stock (Foil, 1989). Visual cues are a key part of landing success for biting flies in the later stages of host location (Egri et al., 2012). Furthermore, Turner and Invest (1973) showed that Tsetse flies are less attracted to objects without a solid silhouette, one that is thought to be broken up by the zebra's pelage. Whilst there is understandably an emphasis on visual cues in work on ectoparasites, olfactory cues are of equal, if not greater, importance allowing the location of prey over long distances (Phelps and Vale, 1976; Blahó et al., 2013). Indeed, if zebra stripes reduce parasitism by flies

then selection should have worked on the flies such that they exhibit aversion to the odours of zebras.

It is important to consider that whilst zebra may have evolved striping as a defence against excessive parasitism, they can still suffer greatly from it (Steelman, 1976; Hunter and Moorhouse, 1976; Harris et al., 1987; Foil, 1989; Hall et al., 1990; Moehlman, 2016). This mitigation rather than total prevention is likely a result of co-evolution with parasitic species (Waage, 1979) where the relatively short generational time of parasites compared to that of zebra and other vertebrate prey species suggests that it is unlikely the striping could have totally out-stripped the evolution of counteractive strategies in this evolutionary arms race of hide and seek. However, zebra are not the only available prey species for biting flies that feed on any mammalian species within their range (Jordan, 1986). Zebra often being found near other large herbivores (Klingel, 1969; De Boer and Prins, 1990), which suggests that their stripes could afford them suitable protection from ectoparasites when foraging in mixed species groups by being a less preferable host. Again, a comparison between the number of flies attacking zebras compared to other sympatric herbivores would be valuable.

A popular counter-argument to this hypothesis is that made by Ruxton (2002) and later reinforced by Gosling (2017) based on work on mountain zebra (*Equus zebra*). They suggest that as this species, which features similar pelage to the plains zebra, is only found in areas with typically low ectoparasite densities (Kingdon, 1977) stripes cannot have evolved in response to ectoparasites. This argument is countered by the work of Lea et al. (2016) that shows that the mountain zebras' range is that of a refugee species resident in a fraction of their historic range in which they would have encountered much higher densities of biting flies. It also ignores the fact that striping could have evolved on an ancestral zebra under selective pressure from biting ectoparasites, but then mountain zebras moved to new areas with low ectoparasite loads that lacked any selective drivers to lose the stripes.

2.5.1 Field and laboratory experiments

Studies utilising experimental setups, whether in the field or laboratory, have provided progressive insights. Some of the earliest works investigating the ectoparasite avoidance hypothesis have produced some informative results, with Waage (1981) utilising a variety of patterns and showing reduced attraction to striped surfaces. Later studies have improved the experimental setup employing new techniques such as sticky traps allowing for a far greater number of replicates for the same sampling effort (Hall et al., 1998). Later studies have built upon this by introducing more physiologically accurate replicas and olfactory cues by utilising tanned hides and bodily fluids (Blahó et al., 2013), with some using the preserved hides of zebra along with those of other sympatric ungulates to compare ectoparasite burdens between the two (Caro, 2016). By using hides, these studies are arguably an improvement on those using painted synthetic materials, as they accurately replicate the light reflected from the animal's pelage. However, as the methods of preservation are not often indicated, there may be variation in olfactory cues - a major part of host location - and this may possibly confound results. In addition, studies using preserved hides often have a very limited number available for use thereby restricting the

variation of patterns that can be tested. Alternatively, synthetic materials can be designed with great precision to mirror a range of natural patterns, and incorporating odour cues.

In the field, the work of King and Gurnell (2010) investigated the impacts of ectoparasitic biting flies on domestic (*Equus ferus caballus*) and Przewalski horses (*Equus ferus przewalskii*), a wild equid found in social groups much like the plains zebra. It is one of the few relevant ectoparasite studies that examines a wild population whereby both olfactory and visual cues were present, with a reasonable sample size of up to ninety individuals over a two-year period. The most recent published research in this area is that of Caro et al. (2019) who studied the effect of striped versus plain pelage on tabanids, using plains zebra and domestic horses (*Equus f. c.*) with striped horse blankets. They found that flies were less successful in landing on the striped surfaces. This is already known from previous work (Waage, 1981), however this study provides new insight into the effect that striping has on biting flies by reducing their deceleration and causing them to crash into or miss the surface of the animal entirely. Interestingly this study also expands indirectly on the work of King and Gurnell (2010) by recording the comfort responses – movements by zebra that are designed to dislodge feeding biting flies. Caro et al. (2019) went further to determine the effectiveness of these behaviours in dislodging ectoparasitic biting flies. Further to this, the work of Horváth et al., (2019) demonstrated that striped body painting, reminiscent of zebra stripes, results in reduced horsefly parasitism in humans, especially where colour contrast is greatest. These studies do not, however, replicate the reflective properties of the zebras' body hair as the horse blankets are made up of fabric, therefore potentially omitting control of a key component of short-range host location important to landing success (Egri et al., 2012).

2.5.2 Comparative studies

Spatial and temporal scales have been a restrictive factor in previous research into the pelage of zebra. The work of Caro et al. (2014), which models the presence of striping in equids and the presence and activity of biting flies on a global scale addresses this deficiency in geographic range. This study also ensures suitable sample sizes with a minimum of seven individuals sampled from each subspecies considered. The study found that there is a positive correlation between the presence of ectoparasitic biting flies that have the potential to represent significant fitness costs (Steelman, 1976; Hunter and Moorhouse, 1976; Harris et al., 1987; Foil, 1989; Hall et al., 1990; Moehlman, 2016) and striping in equids. This result is important to the field as it provides support for the ectoparasite hypothesis at a global population level.

2.6 The directionality and morphology of striping

By looking beyond metrics such as total stripe counts towards the morphology and patterning in the zebra's pelage, the work of Waage (1981) and Gibson (1992) shows that horizontal stripes are least attractive to biting flies. Such horizontal striping is found on the legs of zebra at a height on the body commonly selected for feeding by biting flies on mammalian species due to the density and surface proximity of blood vessels (Kangwagye, 1976; Thomson, 1987). However, the reduced level of striping on the inside of the legs and

belly of the zebra suggest that these areas may be afforded less protection by striping. Despite the lack of consistent or direct sunlight to these areas due to their orientation, these are common feeding sites for biting flies (Britten et al., 2016). This suggests that more visible areas on the outsides of the legs may be receiving protection from biting flies through the confusion of visual cues by striping despite better overall visibility.

The benefits of horizontal striping then seem to nullify the existence of the vertical striping in zebras as it is less advantageous. However, it may be that the developmental process through which stripes form, as pigments move away from the spinal trunk in the foetus, does not allow the formation of horizontal stripes on the rest of the body purely due to orientation. This seems unlikely given the presence of horizontal body stripes in a range of small ungulates (Castello et al., 2016). There are several other potential explanations. It could be that having vertical rather than horizontal striping over such a large area is of greater benefit through its effect on another factor, such as predation risk or thermoregulation, rather than in reducing ectoparasite burdens. Alternatively, it may be that developmentally such a degree of horizontal striping across the body has yet to occur in zebra and may present in the future.

2.7 A developmental artifact?

A thought less discussed is that striping in zebra is merely an evolutionary artifact that has no specific advantage. It could be a result of a past population bottleneck, amplified by a founder effect leading to the expression of striping becoming more prevalent. This theory has been widely dismissed as it seems unlikely that stripes would evolve without a selection pressure causing the trait to be perpetuated in the population (Caro, 2016). Further support for the dismissal of striping as an artifact is found in the similar colouration in other species, not only other equids such as Przewalski horses where faint leg striping is often seen, but in more vivid cases in less related ungulates such as that of the okapi (*Okapia johnstoni*) and zebra duiker (*Cephalophus zebra*) both of which express similar colouration and pelage patterning to the plains zebra, although to a lesser degree (Castello et al., 2016). It is arguable that such complex colouration is exceedingly unlikely to have appeared in such distantly related species which share no common striped ancestor to not have an adaptive advantage. Furthermore, it could be suggested that the orientation of striping - vertical on the body, as it is in the zebra duiker (Castello et al., 2016), and horizontal in the legs as in the okapi (Castello et al., 2016) - is simply the product of embryonic development. During embryonic development, as limbs branch out from the trunk of the body, the direction of striping changes rather than a direct selection for directionality in striping. However, it holds that these changes in the directionality of striping with the sequential development of the embryo is as it is today because of natural selection removing other arrangements of striping from the gene pool.

There are further less discussed advantages offered by colouration such as shown by the work of Lerner and Cage (1973), that domestic horses with pale colouration are more susceptible to developing melanomas and tumours. It could be suggested that a higher level of dark striping in pelage has been selected for, in part at least, because of increased mortality in individuals with a greater amount of white or light pelage. However, this is not a

common hypothesis within the literature and lacks any supporting evidence, though it may provide an advantage as part of the previously mentioned multi-hypothesis approach to striping and could be easily tested using sympatric domestic equids.

2.8 Conclusion and aims

The current evidence is inconclusive in support of any one hypothesis on the drivers of striping in zebras. It may therefore be the case, as is so common in ecological systems, that the lack of evidence for any one hypothesis results from a multi-faceted answer where several contributing factors combine to make a whole, a common occurrence in ecology as discussed by Stephens et al., (2014). Despite this potentially complex answer, it remains important to tackle this area of study pragmatically and attempt to test the already gathered findings. In this case, the ectoparasite hypothesis presents the approach with the most positive findings and therefore the strongest base to provide support for, or indeed expose weakness in, when applying a method that thoroughly considers the previous research onto a large population.

This study investigated the ectoparasite hypothesis on a wild population of plains zebra (*E. quagga burchelli*) in Addo Elephant National Park, South Africa. Recordings of behaviours determined to be a response to irritation from ectoparasitic biting flies were used in combination with data on striping across several regions of the body, hereby referred to as comfort behaviours. Environmental variables that have previously been shown to effect ectoparasitic biting fly abundance and activity were also considered. Striping measures for each region of the body were used in isolation from and combination with each other and environmental variables to if these are a factor in the occurrence and intensity of ectoparasite comfort behaviours. This study aimed to determine whether expected reductions in ectoparasites on zebra, and so ectoparasite comfort behaviours, with increased striping are consistent across a large population under similar environmental conditions.

3.0 Methods

3.1 Study site

Addo Elephant National Park (Addo), located in the Eastern Cape Province of South Africa, covers an area of ~1640km². It is the country's third largest national park and is operated by the South Africa National Parks authority (SANParks, 2018). The park boasts a large population of African elephants (*Loxodonta africana*) along with high densities of Cape buffalo (*Syncerus caffer*) and sizeable populations of a range of other large herbivore species, including ~600 plains zebra (*Equus quagga*), and a notable population of the IUCN Red Listed mountain zebra (*Equus zebra*) in the mountainous northern Zuurberg section of the park (SANParks, 2016). The plains zebra in the park were introduced in 1984, 30 years after the erection of the Armstrong elephant fence, which encloses the park (SANParks, 2018). This reintroduction was part of the Quagga Project breeding programme, which attempted to back-breed plains zebra to produce what is now understood to be the extinct Quagga subspecies (*Equus quagga quagga*) (Harley et al, 2009). Because of this programme, the plains zebra population in Addo is thought to have a higher than average degree of variation in striping than other populations, making them an ideal study population when investigating the factors hypothesised to have brought about the evolution of the zebra's distinct pelage.

The park is comprised of four sections that include coastal, mountainous, and plains habitats - all of which experience year-round semi-arid conditions with low levels of rainfall and relatively high temperatures. This study sampled individuals in the "Colchester" and "Main Camp" sections of the park, between which animals can move freely since the removal of divisionary fencing in 2010. A large proportion of this area is made up of thicket biome, comprising largely of spekboom (*Portulacaria afra*) among other dense, thorny vegetation. The large elephant population in the park has helped to maintain areas of open grassland that were historically created for agriculture, and opened up areas of thicket through trampling and herbivory, particularly around man-made waterholes as there are no natural year-round water sources in the park (Lombard et al., 2001; Davies et al., 2017).

3.2 Study species, the plains zebra (*Equus quagga burchelli*)

This project's study species is the *burchelli* subspecies of the plains zebra (*Equus quagga burchelli*), a large ungulate native to sub-Saharan Africa with this subspecies being found in the more southerly regions of the continent (Groves and Bell, 2004). Animals can weigh over 330 kilograms, with little obvious sexual dimorphism in their proportions (Fischhoff et al, 2009). Zebra are well known for their distinctive pelage, made up of a black coat with white stripes (Prothero and Schoch, 2003). Zebra are an extremely social species, like many other large herbivores, aggregating into groups with conspecifics and other species to a lesser extent (Klingel, 1968). In zebra, these groups form part of a complex multi-tiered social system with sub-groups of various demographics and roles within a larger population.

3.2.1 Social system of the plains zebra

The base unit of a population is the harem, consisting of up to eight females and their dependent or immature young under the protection of a single dominant stallion. These family groups are very stable in their structure with movement of mature females out of the harem being extremely rare (Klingel, 1965; Rubenstein, 1986 and 1994a). Young born to the group usually disperse within three years (Klingel, 1965). When reaching sexual maturity females are abducted by mature males from outside the family group and taken into another harem, typically occurring within the first two years (Klingel, 1965). Young males disperse to form their own harems or join bachelor groups up to a year later, at around three years of age (Klingel, 1965). Bachelor groups are comprised of up to fifteen males banding together for safety before either forming their own harem or after being ejected from an existing group. Outside of these groupings are sometimes found lone males either moving between their natal group and a bachelor group or harem, or former stallions that have been ejected from their harem by a usurper (Rubenstein, 1994a). Lone males do not remain in this lone state for long due to the increased risk of predation in the absence of conspecifics. The largest of zebra aggregations are often termed “herds” (Rubenstein, 1994b) that are made up of smaller social groups at times where the reduced predation risk from conglomerating in this way outweighs the increased competition for resources. This often occurs when moving over large distances during migration or during period of high yields of vegetation (Rubenstein, 1994b).

This multi-tiered social system with stallions dominant over large numbers of breeding females has the capacity to perpetuate beneficial phenotypes, facilitating genetic drift as a product of sexual selection within the social groups that make up the wider population (Wright, 1943 and 1946; Clegg and Phillimore, 2010; Orsini et al., 2012). However, the movement of animals between groups through the usurping of harems by fitter males, the abduction of young females, or sneaky mating are likely to have detracted from genetic drift, although maintaining genetic diversity, through the addition of genetic information from a greater number of individuals into the available gene pool.

3.3 Previous methods for the quantification of striping

The basis of any works investigating the functional role of striping hinges not only on the measurement of external factors but also the quantification of striping. Several methods have been used previously ranging from: a simple sum of all stripes on an animal’s body as used by Harley in his stripe scoring system (Harley, 2009); to the use of categories for the relative intensity of striping in different body regions (Caro, et al., 2014). Many studies reduce the detail provided by these indices by grouping different frequencies of stripes into broader categories, although they often maintain separation between regions of the body therefore allowing comparison of differing effects across the body. Harley’s stripe scoring system does not reduce the precision of the data in this way when left unmodified and allows the comparison of different body sections or the whole body. This depth of detail has been shown to be important in the work of Caro et al (2014) whereby the intensity of striping on the legs across several species of equid was shown to correlate with potential ectoparasitic burdens. This work is proof that precision in stripe scoring is important to

allow for the comparison of the total degree of pelage variation across a population, whilst also enabling the investigation of variation between body regions.

An aspect of zebra pelage often overlooked is that of background colouration, which often seems purely black and white. This potentially leaves a hole in datasets that are not considering possible variation in contrast - surely a central part of any hypothesis considering the visible effects of colouration. Few studies quantify “shadow-stripping”, which is another information gap.

A key feature the zebras’ pelage is that stripe patterns are unique to individuals (Petersen, 1972) and can therefore be used for identification. This has been utilised by several studies to identify individual animals from images captured in the field (Klingel, 1965; Klingel and Klingel 1966), as well as being used to develop identification systems usable in the field (Petersen, 1972). This can however be extremely time consuming if carried out to a great level of detail. Conversely if over simplified it can limit sample size if working in a large population. The development of modern techniques that employ complex algorithms, such as the software stripespotter (Lahiri et al., 2011), are able to identify individuals from digital photography greatly increasing both the speed and scale at which a population can be identified at an individual level.

3.4 Materials and methods

Fieldwork was undertaken for a period of 58 days with the initial task being populating a photographic database containing each of the plains zebra within the park. Images of both flanks, head, and rump were captured from a vehicle driven on marked tracks using Canon EOS® 400 and 550 models principally with Canon EF-S 55-250mm f/4-5.6 IS and EF 100-300mm f/4.5-5.6 USM telephoto lenses. Upon sighting study animals, a group location was recorded consisting of UTM coordinates using a Garmin Etrex® 10 along with, distance to the centre point of the group using a Nikon® laser reflective rangefinder, and a compass bearing relative to the direction of the vehicle with a GWHOLE® sighting compass. This allowing for accurate recording of location.

Habitat was recorded as one of three categories: grassland, scrub, or thicket. These categories were differentiated estimating dominant vegetation type by area, with grassland containing 70% or greater grasses, scrub comprised of between 70% grasses and 70% woody vegetation, and thicket comprising greater than 70% woody vegetation. Number of individuals, sex, and age were then recorded with the aid of binoculars, spotting scope, and photography. Sexes were differentiated using the distinct difference in area of dark pigmentation around the anus and genitalia where females have a much larger area encompassing both anus and genitalia, and where possible external genitalia were used for initial identification; or confirmation in challenging cases (Figure 1). Animals were categorised into adults and juveniles, determined by body size, shape, and pelage characteristics with very young juveniles being distinguishable by large numbers of long guard like hairs. Older juveniles or sub-adults close to two years of age were difficult to distinguish reliably from adults and so were grouped together due to sampling rate and time limitations per group. Mother-foal relationships were identified through behavioural

observations, primarily nursing. Pregnant females were identified through visual observation of distended abdomens, oval in shape when observed from front or back, showing a well-developed foetus, through swelling of the mammary glands or evidence of lactation. Stallions were identified through behavioural observation and group demographics. Group types were categorised into harems, bachelor groups, or mixed herds based on the group's demography and size.



Figure 1. Posteriors of male (left) and female (right) plains zebra differentiated by the area of dark pigmentation under the tail. Male genitalia often blend with the dark ventral stripe at a distance making this an unreliable indicator unless obvious.

In the field, group sightings were given a unique group code with individuals being numbered sequentially within each group. Images for each flank, front and back were captured and assigned to each individual, with aging and sexing being conducted alongside this. At least one team member maintained constant visual contact to ensure individuals were not misidentified during movement. Minimum standards of visibility and distance were set based on the quality of images that could be obtained, in borderline cases test images were taken and a decision was made by the three researchers collectively on whether to include the observation. Pseudoreplication caused by resampling the same individuals was minimized by alternating between the Colchester (Southernly) and Main Camp (Northernly) sections of the Park each day, moving throughout areas quickly to avoid coming across the same herd at two nearby points, and only sampling an area once in a day. Each day's sampling typically lasted 4-8 hours dependent primarily upon the number of animals encountered throughout the day.

3.4.1 Stripe-scoring

Images were entered into Stripespotter (Lahiri et al., 2011), an opensource database designed to identify unique individual zebra using pattern recognition to interpret pelage patterns. This database was also used to detect replications within the database prior to

analysis of the data. Striping was quantified using a modified version of Harley's stripe scoring method, by counting the number of black stripes on standardized body segments (Harley et al., 2009). These sections were broken down into eight regions as informed by the work of Groves and Bell (2004) and later that of Caro et al. (2014). These sections were face, head, neck, torso, belly, foreleg, hind leg, and rump and were recorded for each flank of the body (Figure 2). The number of stripes and shadow stripes (figure 2) were counted on each of the body regions, in addition the number of stripes on the torso which extended to contact the ventral midline were counted (belly stripes).

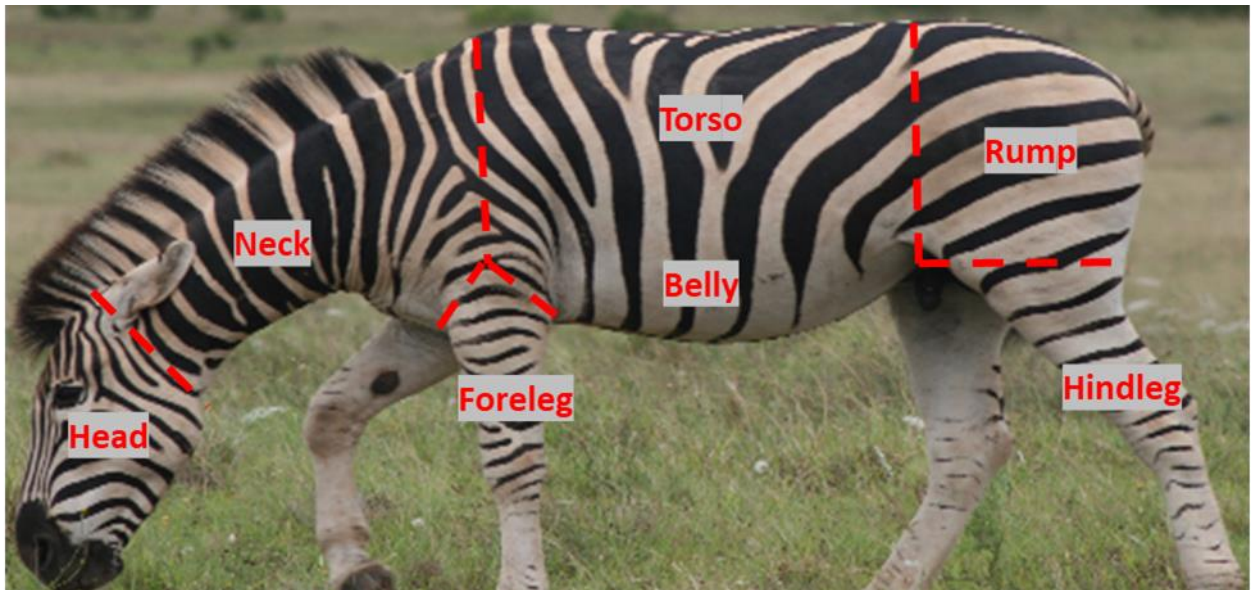


Figure 2. Demarcated body sections into which stripes were grouped and counted.

In addition to stripe counts, other physical traits were recorded including mane and tail length that were categorised into one of four categories ranging from 0 to 3. A tail or mane recorded as 0 would denote an absence of this feature, with each of the following categories 1, 2, and 3 coinciding with the presence of the feature in thirds of total potential length. Background pelage colour was recorded into one of two categories (light or dark) to determine contrast between stripes and their background on each animal, although this was thought to be primarily a product of rolling causing a coating of earth leading to a slight reddish appearance (Figure 3). This variable was found to have no effect on comfort behaviour occurrence and so were excluded from later analyses. Image quality was ranked from 1 to 4 determined based on clarity and the number of visible body sections as follows, where 1 was "all sections present and clear", 2 was "all sections present, not good", 3 was "up to two sections not present or poor" and 4 was "greater than 2 sections not present or poor". Having obtained a suitably large sample of score 1 images, those with a score 2 or greater were excluded from analysis.



Figure 3. A comparison of clean and dirty background colouration.

3.4.2 Ectoparasite data

The ectoparasite hypothesis was tested using behavioural observations as a proxy for ectoparasite burdens. These included any behaviours that were thought to be in response to irritation by ectoparasitism from biting flies. This took the form of comfort behaviours formulated by expanding on the methods of King and Gurnell (2010) in similar work on the Przewalski's horse, and which were concurrent with those used by Caro et al. (2019) on zebra and domestic horses published after our data collection. Where possible, each individual animal within a group was sampled, undergoing focal sampling for five minutes, recorded using a Canon eos 550D with 55-250mm USM IS lens. Video recording was essential as many comfort behaviours occurred simultaneously making accurate recording of all relevant behaviours in the field challenging. These categories were head toss, ear flick, skin ripple, tail swish, stamping, body shake, facial rubbing (typically rubbing the face against the forefoot or leg), rubbing on an object, rolling, and self-grooming. Both the frequency and duration of each incident of these behaviours were recorded. The data from the animals sampled in this will be referred to as the ectoparasite sample or subset.

3.4.3 Analysis

Comfort behaviour categories were refined down from the original behaviours to a new set of seven categories based on their relevance to each striping region (Table 1). For example, head tossing and ear flicking were combined into head comfort as head striping could not be split into a standardised region for each of the original behaviours due to lack of reference points and morphological differences in striping. These new categories were then adjusted to provide a standardised total duration of behaviour per minute by combining the duration of each incident within each behavioural category. In cases where recordings were not a standard duration (300 seconds), they were also included in this adjustment to a per minute metric, if within the range of 150 to 450 seconds, accounting for 62 of 238 samples. Distributions of the data for each variable were determined using visual representation with histograms.

The data were analysed using linear mixed effects models with a normal distribution in the R Statistics software package (v3.4.3) (R Core development team, 2008) using the lme4 package (v1.1-19) (Bates et al., 2015). Initially, prior to the use of mixed modelling, relationships between dependent and independent variables were investigated using correlations. Fixed effects consisted of environmental variables which had previously been shown to impact ectoparasites in some way – these being air humidity (%), air temperature (Celsius), light intensity (lumens), and wind speed (metres per second) - and stripe counts for body regions (Figure 2). Each model contained the unique numeric identifier of each animal as a repeat measure (random effect). A series of candidate models were constructed for each behaviour category as the dependent variable. Each series of candidate models included a null model. These candidate models were then compared using AICc (Akaike’s Information Criterion adjusted for small sample size) to remove poorly performing models (Akaike, 1973; Akiake, 1974). The top performing models, those within the top 0.95 of AICc weight (AICcWT), providing the top 95% of support were retained. Each fixed effect present in the remaining models then underwent model averaging using the AICcmodavg package (v2.2-1) (Mazerolle, 2019) to produce effect sizes (β). Used to determine whether any of the variables had a significant effect in explaining the variation in behavioural response. Trends between striping categories and environmental variables were plotted as a scatter fitted with a linear trendline and 95% confidence intervals using ggplot2 (v3.1.0) (Wickham, 2016). The relationship between total body striping and the age and sex of zebra was tested using a Two-Way ANOVA.

Table 1. Summary of the categories of comfort behaviours created from combining individuals behaviours.

New behavioural category	Constituent behaviours
Head Comfort	Head toss, Ear flick
Tickle Comfort	Skin ripple, Body shake
Body Comfort	Body rub, Rolling, Self-grooming (biting)
Tail swish	Tail swish
Stamp	Stamp
Body comfort combined	Body comfort, Tickle comfort
Full body comfort	All original behaviours

4.0 Results

4.1 Sample

A total of 1234 animals were sampled across 211 groups over a 58-day period from February – March, 2018. The Stripespotter software package (v2.1 for Windows) (Lahiri et al., 2011) revealed 625 of the total observations were unique individuals based on their pelage patterns. Some 238 unique five-minute behavioural samples were collected from 169 individuals during the survey period, providing data on the prevalence of ectoparasite comfort behaviours. The samples sizes of the total population and those observed for comfort behaviours are detailed below in table 2.

Table 2. Shows the sample sizes (n) of the number of unique individuals within the population (all unique individuals recorded during survey) and those sampled for ectoparasite comfort behaviour (not all individuals are unique) in Addo Elephant National Park, Eastern Cape, South Africa.

Age	Sex	Ectoparasite sample	Population
Adult	Female	106	259
	Male	100	274
	Unsexed	0	7
Juvenile	Female	18	45
	Male	13	36
	Unsexed	1	4

4.2 Striping

Striping within the population was normally distributed across the body of the plains zebra sampled. Neck and torso striping exhibited a negative skew, with a positive skew found in belly and head striping. Stripe count across each side of the body was strongly related overall ($R = 0.78$, $n = 616$, $p = <0.01$), as well as separately in adults ($R = 0.77$, $n = 531$, $p = <0.01$) and juveniles ($R = 0.88$, $n = 85$, $p = <0.01$). There was also no significant difference between mean total striping in unique individuals ($n = 625$) and those sampled in the ectoparasite subset ($n = 238$) (figure 4). Therefore, the ectoparasite subset is representative of the entire population in its level of striping.

Within the population, mean striping varied significantly with age (with a greater number of stripes in juveniles) ($F(1) = 10.32$, $p = <0.01$) and sex ($F(2) = 12.02$, $p = <0.001$). There was no interaction between age and sex ($F(2) = 1.967$, $p = 0.14$) (figure 5). Full ranges and mean striping and shadow striping for each body region and stripe type are shown in table 3. Mean total body striping showed no significant relationship with head ($R = 0.16$, $d.f. = 213$, $p = 0.12$), full body ($R = 0.1$, $d.f. = 213$, $p = 0.15$), and tail swishing ($R = 0.09$, $d.f. = 213$, $p = 0.17$) comfort behaviours (figures 7, 9, and 10 respectively). Head comfort behaviour was not related to head striping ($R = 0.05$, $d.f. = 213$, $p = 0.44$) (figure 9).

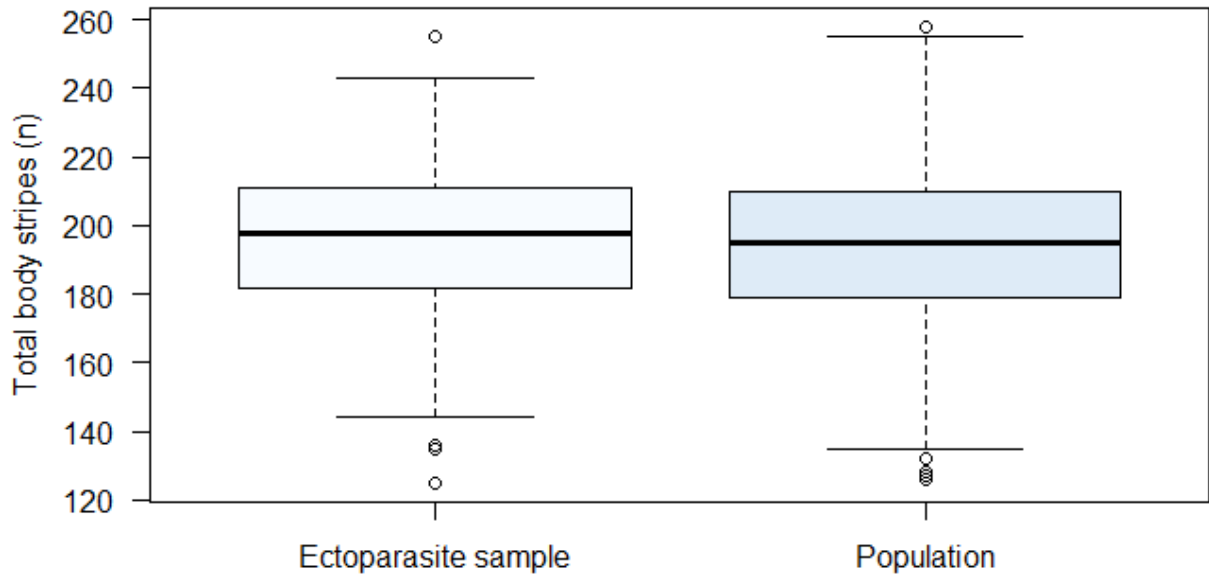


Figure 4. Box plot of the mean total body striping of individuals sampled for ectoparasite comfort behaviour (Ectoparasite sample) and the population (Unique individuals) in plains zebra in Addo Elephant National Park. Median value displayed within the IQR, data outside the Q1 – Q3 range are plotted as outliers (o)

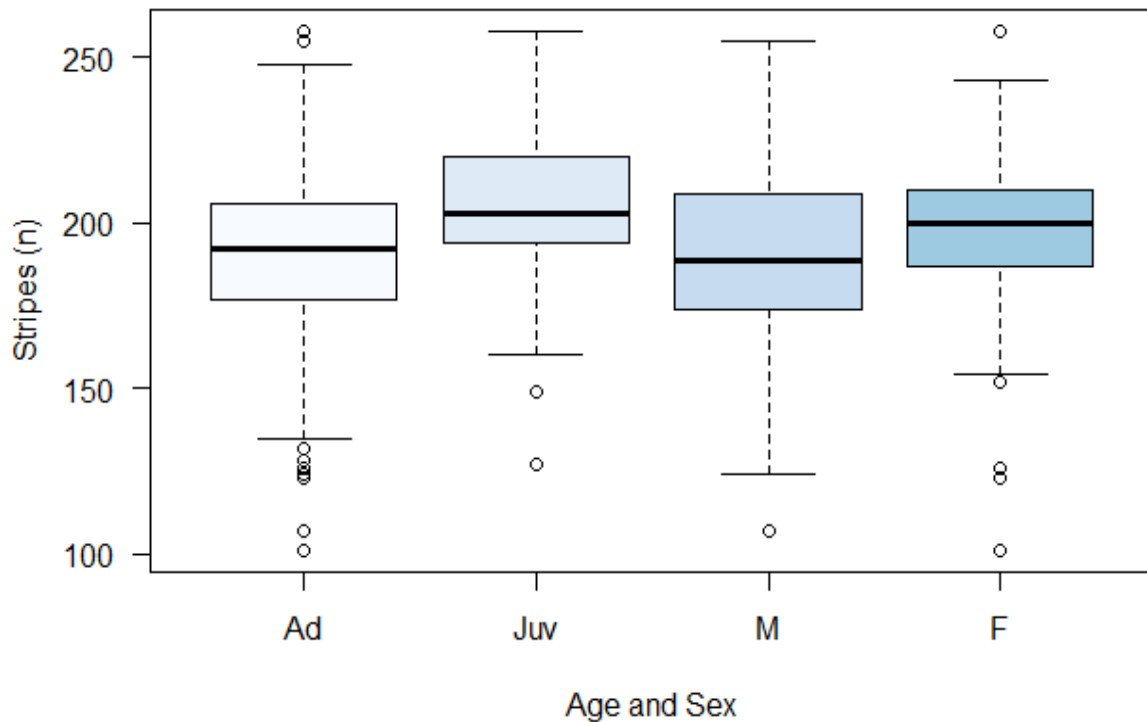


Figure 5. Box plot of the mean total body striping in age and sex categories in plains zebra in Addo Elephant National Park. Categories are as follows: adults (Ad), juveniles (Juv), males (M), and females (F). Median value displayed within the IQR, data outside the Q1 – Q3 range are plotted as outliers (o)

4.2.1 Rump striping

Rump striping was distributed bimodally with the largest number of animals having between zero and two stripes on the rump, the remaining individuals showed values clustered in the region of two to fourteen stripes (median eight to twelve) (Figure 6).

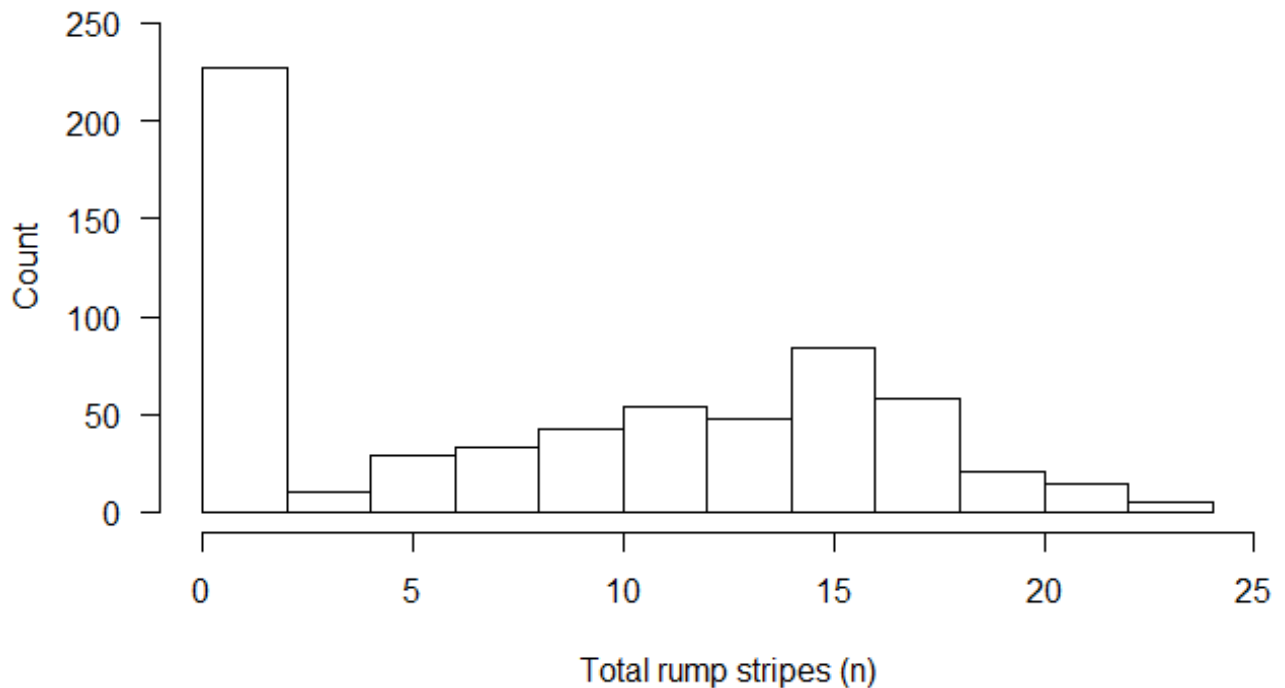


Figure 6. Histogram of rump striping of individuals within the plains zebra population of Addo Elephant National Park where a high proportion had two or less stripes on the rump.

4.2.2 Shadow striping

Shadow striping was normally distributed (Figure 7) and was most prevalent on the legs and torso with a maximum of 43, 40, and 25 for foreleg, hindleg, and torso respectively. Shadow striping did not have a significant effect on any ectoparasite comfort behaviour. Regular and shadow striping in the population is detailed in Table 3 below.

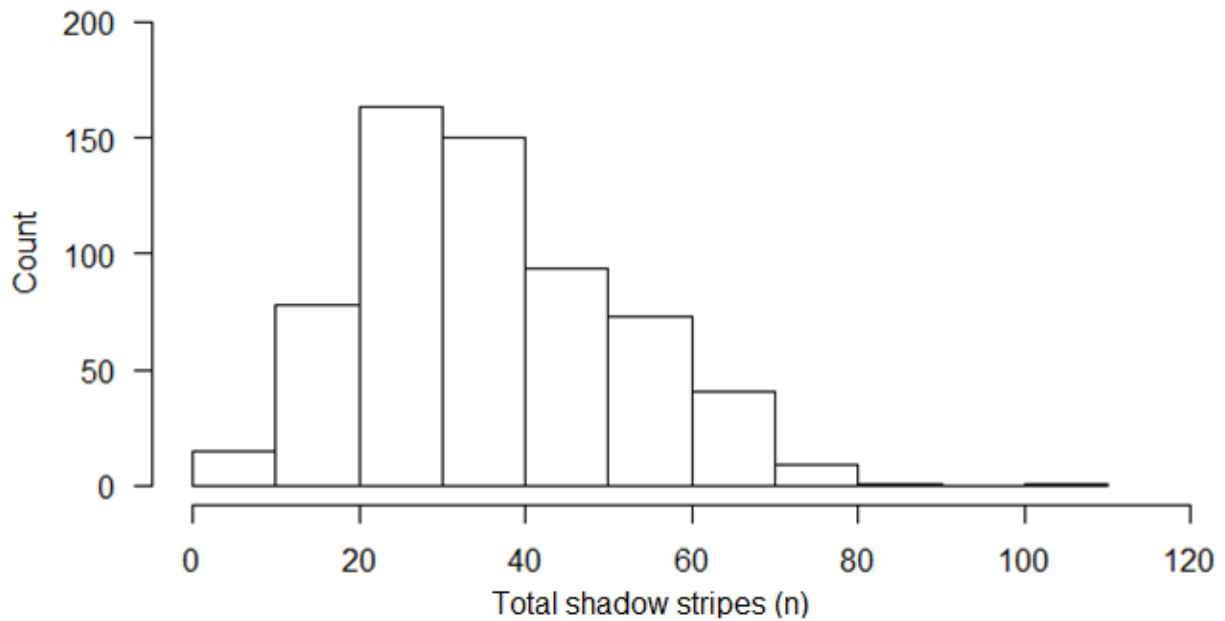


Figure 7. Histogram of shadow striping across the body was distributed normally in plains zebra in Addo Elephant National Park.

Table 3. Ranges of stripe count for each region of the body (as set out in figure 2).

Region	Regular stripes			Shadow stripes		
	Min	Max	Mean	Min	Max	Mean
Full body	101	257	196.1	0	90	28.2
Head	16	53	39.3	0	6	0.1
Neck	14	57	36.6	0	19	1.9
Torso	14	55	34.9	0	25	6.7
Belly	0	17	9.2	0	8	0.2
Foreleg	13	64	37.4	0	48	8.0
Hindleg	12	61	38.9	0	40	6.5

4.3 Ectoparasite removal behaviour

Ectoparasite removal behaviour and changes therein are presented in units of total duration of the target behaviour or category of behaviours on a per minute basis. The relative occurrence of each of the recorded comfort behaviours and categories are shown below in Table 4. Tail swishing was by far the most common single behaviour with a mean duration of 12.8 seconds per minute across the sample. Across all models, striping was a poor predictor of comfort behaviours with the best performing models selected using AICc being retained in the analysis (Table 5).

Full body comfort decreased with increased wind speed ($\beta = -1.74, -3.13$ to -0.34) and humidity ($\beta = -0.48, -0.71$ to -0.25) (Table 6). Head comfort behaviours were negatively affected by humidity ($\beta = -0.02, -0.03$ to -0.01) and showed an increase coinciding with positive changes in temperature ($\beta = 0.06, 0.03$ to 0.08) (Table 6). Tail swishing decreased with increasing wind speed ($\beta = -1.62, -2.86$ to -0.39) and humidity ($\beta = -0.47, -0.68$ to -0.25) (Table 6).

Table 4. Comparison of mean duration of comfort behaviours (as in Table 1) within the ectoparasite sample (n=238). Demonstrating the prevalence of tail swishing amongst the recorded behaviours.

Comfort Behaviour	Mean duration (second per minute)
Head	0.71
Tickle	0.47
Tail swishing	12.80
Stamping	0.29
Body	0.66
Full Body	14.93

Table 5. The best performing models of zebra (a) full body comfort behaviour, (b) head comfort behaviour, and (c) tail swishing are accounting for ≥ 0.95 of the AICc.

	K	$\Delta AICc$	AICcWt	Res.LL
(a) Full body comfort behaviour time				
Wind speed + Humidity	5	0	0.62	-883.57
Humidity + Temperature + Wind speed	6	1.73	0.26	-883.38
Humidity	4	5.08	0.05	-887.16
Temperature + Humidity	5	6.32	0.03	-886.73
Total striping + Temperature + Humidity + Wind speed	7	6.52	0.02	-884.7
Temperature	4	7.74	0.01	-888.49
Total both hindleg	4	25.89	0	-897.56
(b) Head comfort behaviour time				
Temperature	4	0	0.58	-286.13
Humidity	4	1.59	0.26	-286.92
Wind speed + Humidity	5	4.82	0.05	-287.49
(c) Tail swishing time				
Wind speed + Humidity	5	0	0.63	-860.97
Humidity + Temperature + Wind speed	6	1.65	0.28	-860.74
Humidity	4	5.55	0.04	-864.8

Table 6. The observed relationship of each response variable (a) full body comfort behaviour, (b) head comfort behaviour, and (c) tail swishing and the model-averaged parameters for the top performing models (β estimate \pm 95% CI). Effects with CI's not overlapping zero are highlighted in **bold**. These effects are represented visually in Figures 6 through 16.

	Cum. AICcWt	β	Lower CI	Upper CI	Std. error
(a) Full body comfort					
Wind speed	0.9	-1.74	-3.13	-0.34	0.71
Humidity	0.98	-0.48	-0.71	-0.25	0.12
Temperature (°C)	0.29	0.27	-0.64	1.18	0.47
Total striping	0.02	0.06	-0.03	0.15	0.05
(b) Head comfort					
Temperature (°C)	0.59	0.06	0.03	0.08	0.01
Humidity	0.32	-0.02	-0.03	-0.01	0.01
Wind speed	0.05	-0.08	-0.16	0	0.04
Total neck striping	0.03	0.04	0.01	0.06	0.01
Total striping	0.01	0.01	0	0.01	0
Total neck striping (excl. shadow)	0.01	0.03	0	0.07	0.02
(c) Tail swishing					
Wind Speed	0.93	-1.62	-2.86	-0.39	0.63
Humidity	0.99	-0.47	-0.68	-0.25	0.11
Temperature (°C)	0.31	0.32	-0.48	1.12	0.41
Total striping	0.02	0.05	-0.03	0.14	0.04

4.4 Environmental variables

Environmental variables of wind speed, air temperature and air humidity were plotted against comfort behaviours in linear regression models. Wind speed showed no significant effect on tail swishing ($R = -0.1$, d.f. = 213, $p = 0.16$) or full body comfort ($R = -0.09$, d.f. = 213, $p = 0.21$) (figures 12 and 13). Increases in air humidity coincided with significant reductions in the mean duration of tail swishing ($R = -.035$, d.f. 213, $p = <0.01$), full body ($R = -0.34$, d.f. = 213, $p = <0.01$), and head ($R = -0.26$, d.f. 213, $p = <0.01$) comfort behaviours (figures 12, 14, and 16). Higher air temperatures occurred alongside increases in head comfort behaviour, and these were significant at the 95% confidence interval ($R = 0.22$, d.f. = 184, $p = <0.01$) (Figure 16).

4.4.1 Light intensity

Despite a wide range of luminosity values recorded across the ectoparasite sample, exhibiting a bimodal distribution, and previous evidence suggesting luminosity drives ectoparasite activity (Egri et al., 2012), this variable performed poorly as a predictor throughout model selection. Luminosity was therefore omitted from the finalised set of candidate models.

4.5 Group size and time of day

Although a wide range of group types and sizes were sampled across a large period of the day (06:00 to 17:00) and the large body of research demonstrating that biting fly activity varies with time of day and ectoparasite loads decrease with group size (Freeland, 1977; Rutberg, 1986), these were poor predictors of behavioural activity and were therefore omitted from the analysis.

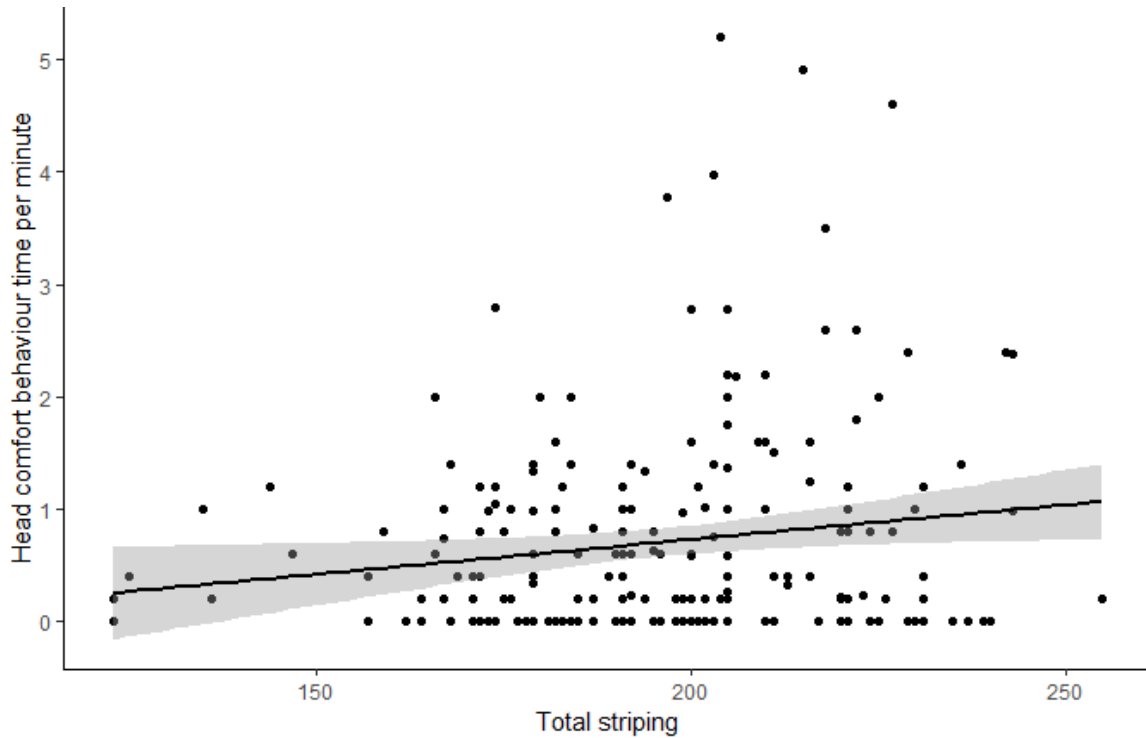


Figure 8. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of total striping and the duration of head comfort behaviour in plains zebra in Addo Elephant National Park.

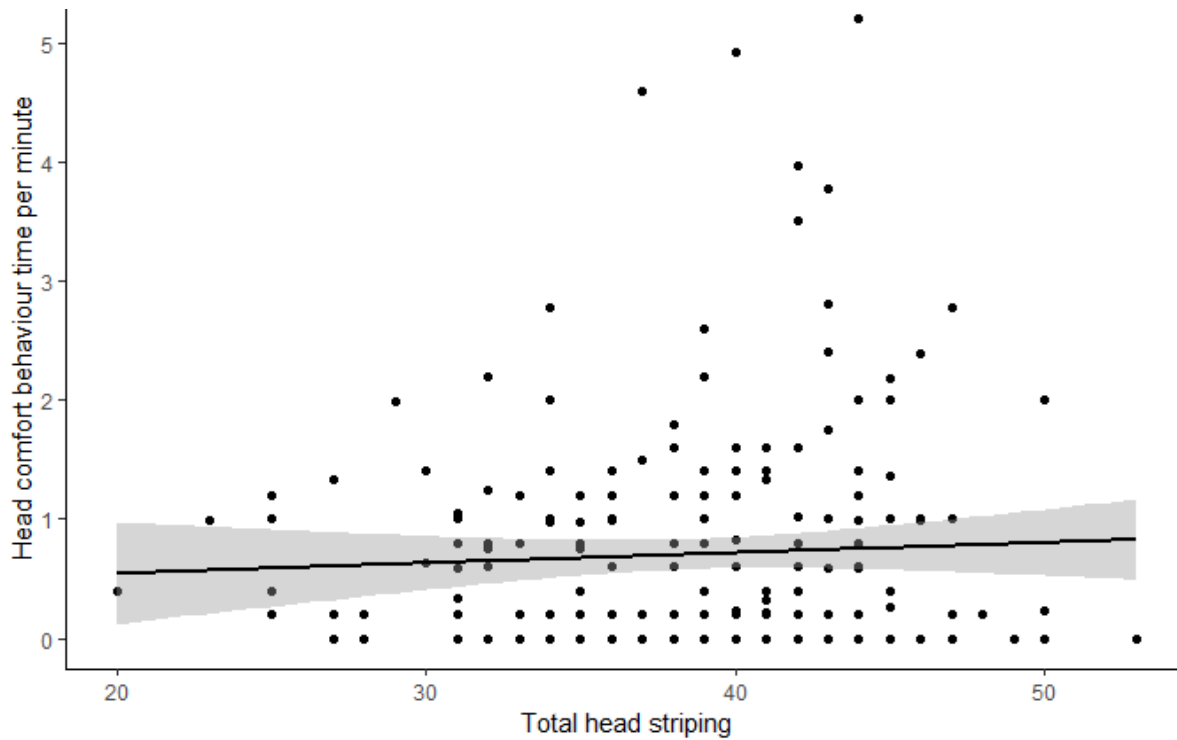


Figure 9. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of total head striping and head comfort behaviour duration in plains zebra in Addo Elephant National Park.

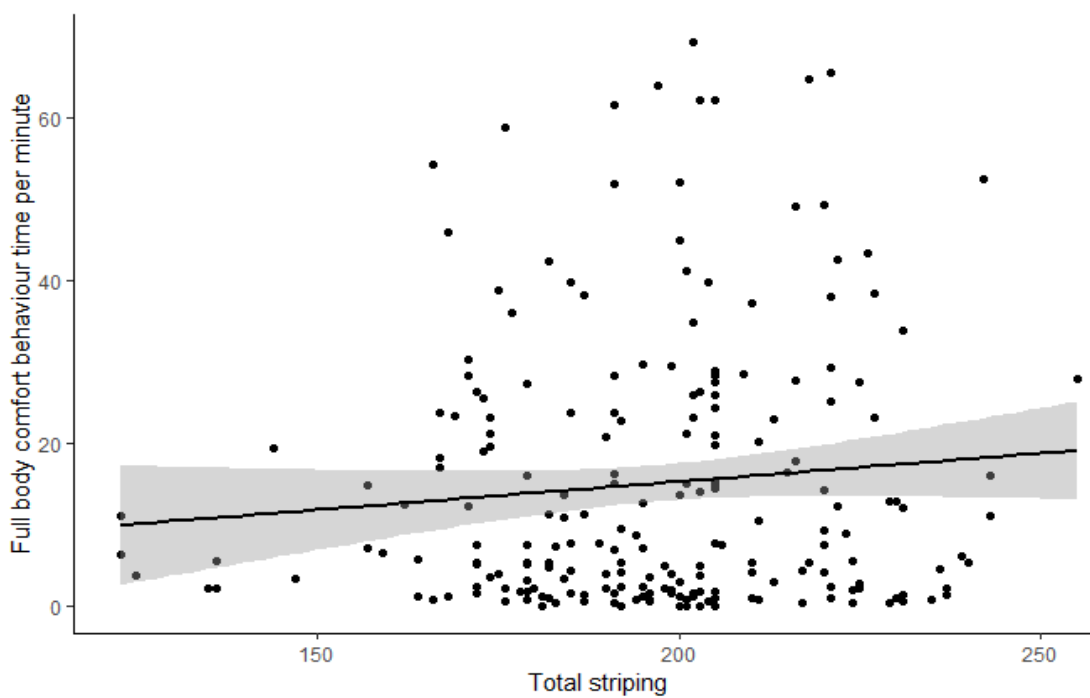


Figure 10. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of total body striping and the duration of full body comfort behaviours in plains zebra in Addo Elephant National Park. The maximum duration exceeds 60 seconds per minute as this is a sum of all behaviours.

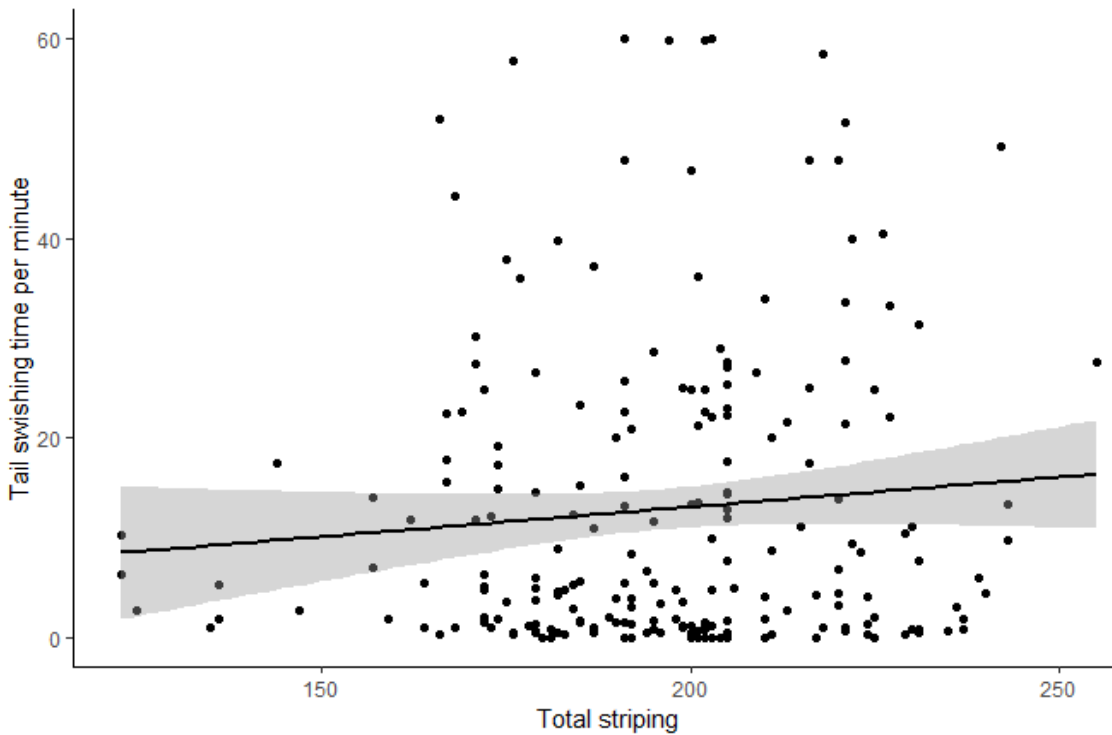


Figure 11. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of body stripes and the duration of tail swishing per minute in plains zebra in Addo Elephant National Park.

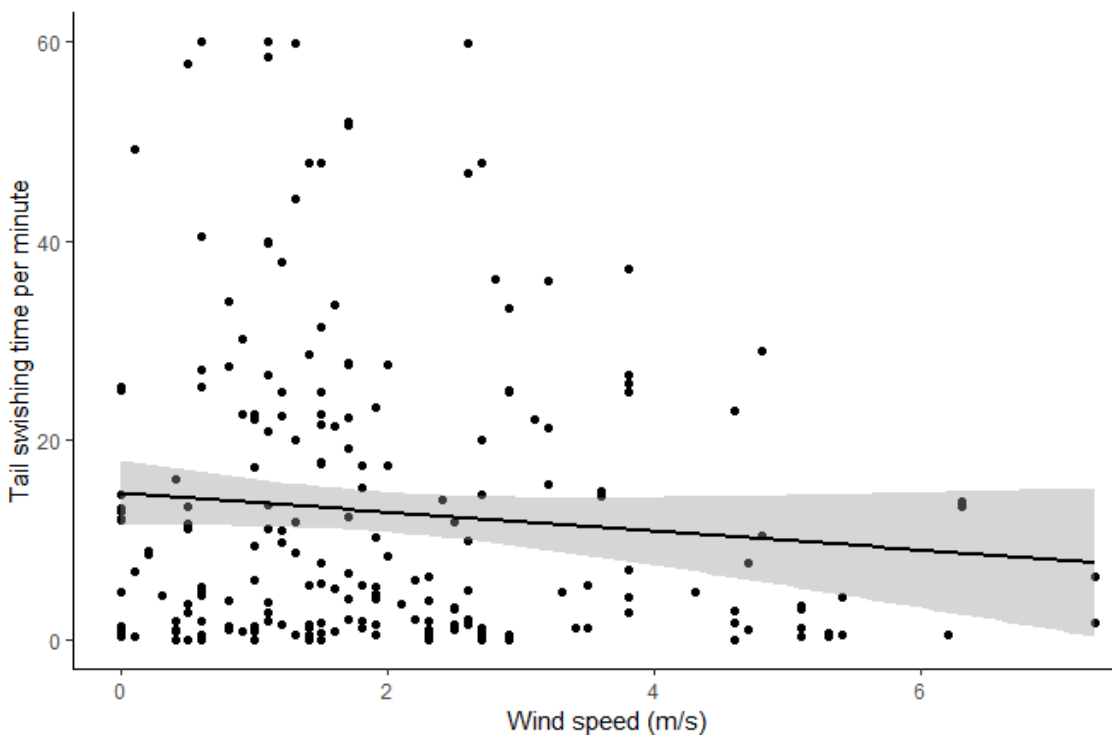


Figure 12. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of wind speed and the duration of tail swishing comfort behaviour in plains zebra in Addo Elephant National Park.

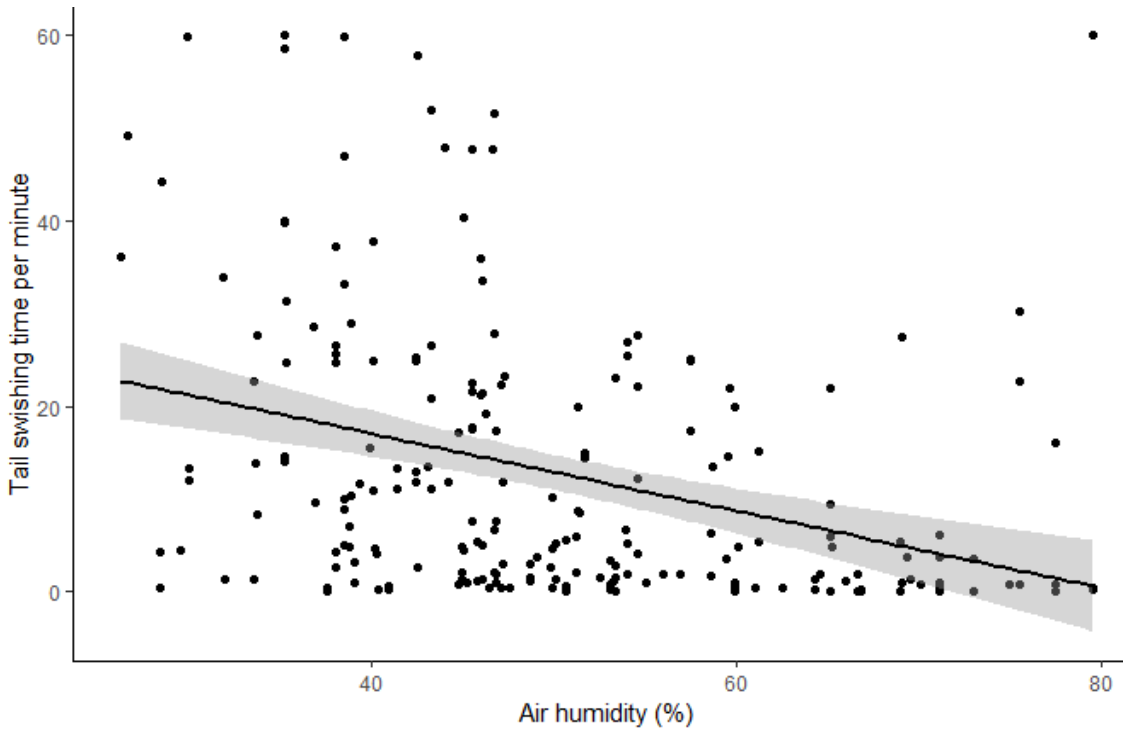


Figure 13. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of air humidity (%) and the duration of tail swishing behaviour in plains zebra in Addo Elephant National Park.

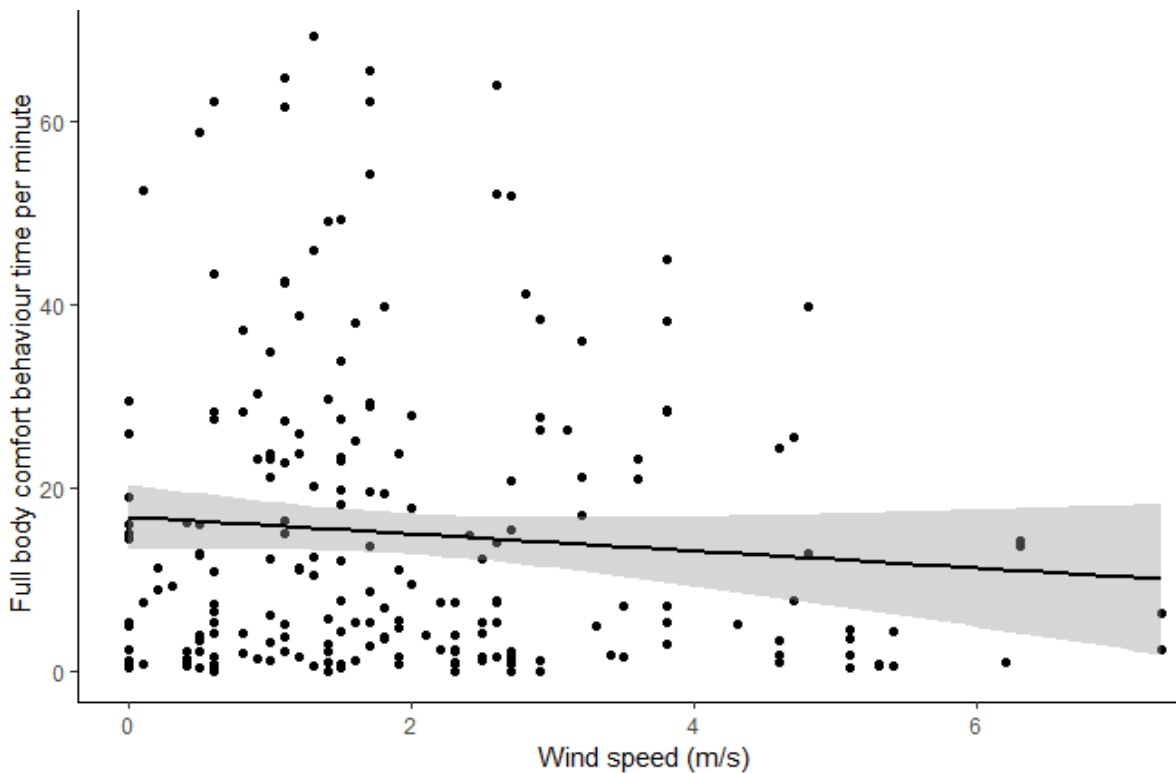


Figure 14. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of wind speed and the duration of full body comfort behaviour in plains zebra in Addo Elephant National Park.

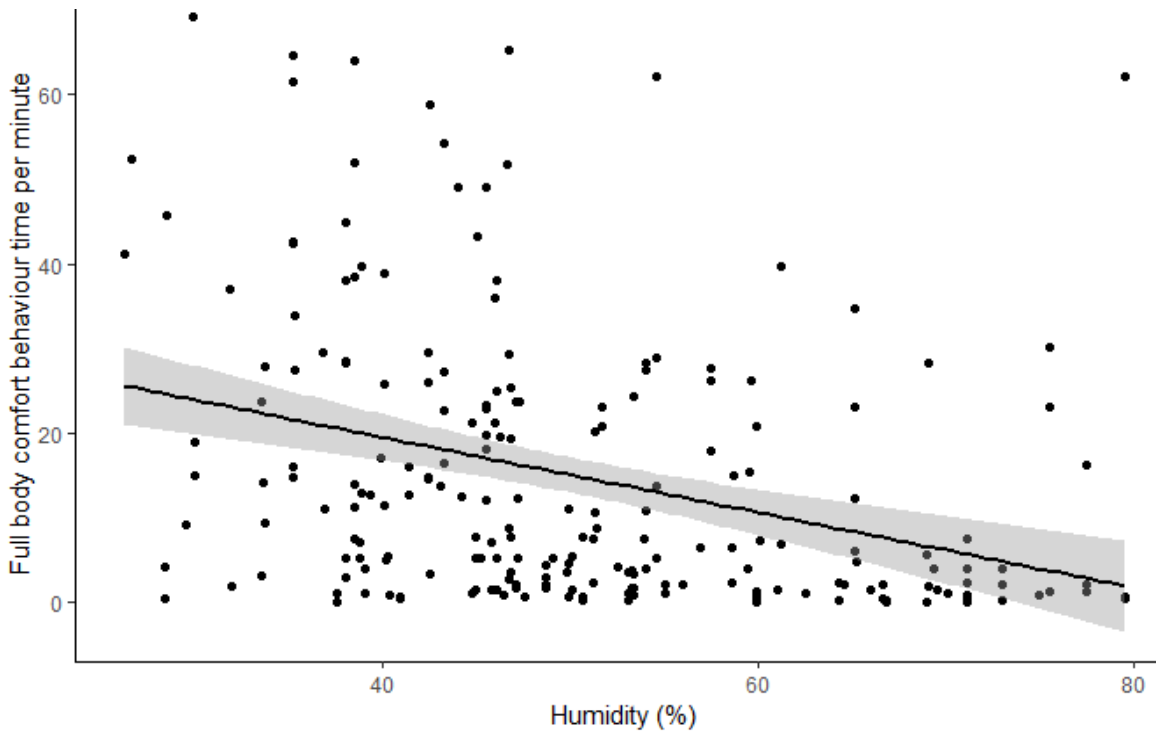


Figure 15. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of air humidity (%) and the duration of full body comfort behaviours in plains zebra in Addo Elephant National Park

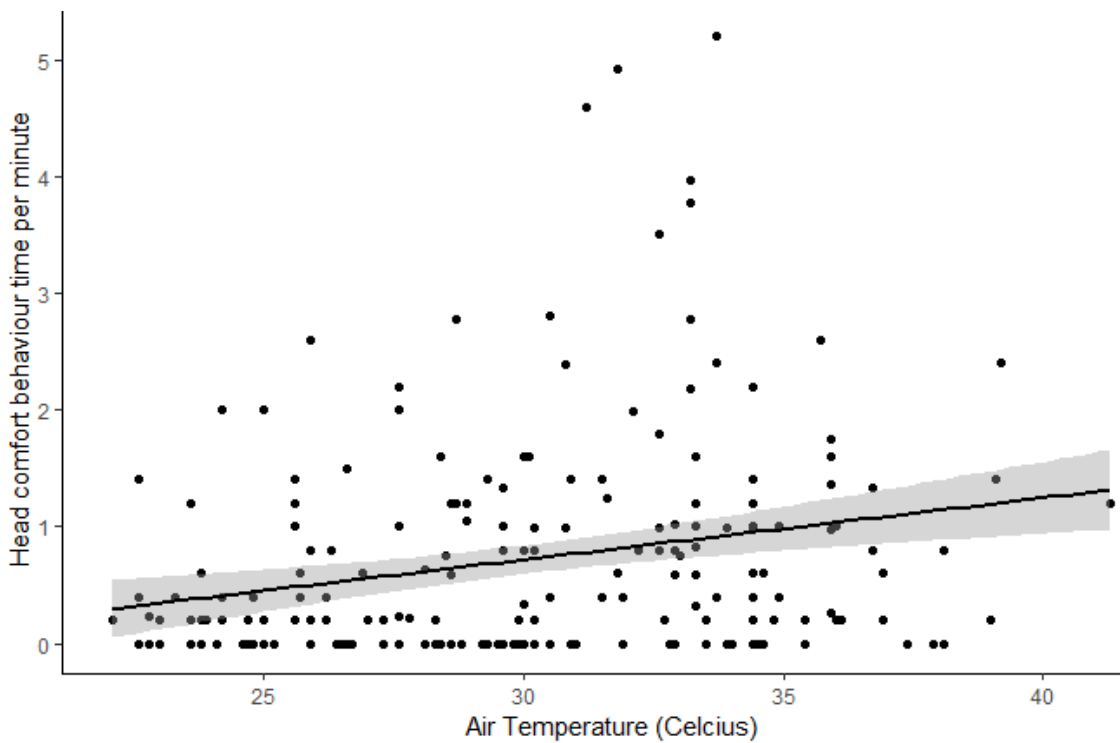


Figure 16. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of air temperature on the duration of head comfort behaviour in plains zebra in Addo Elephant National Park.

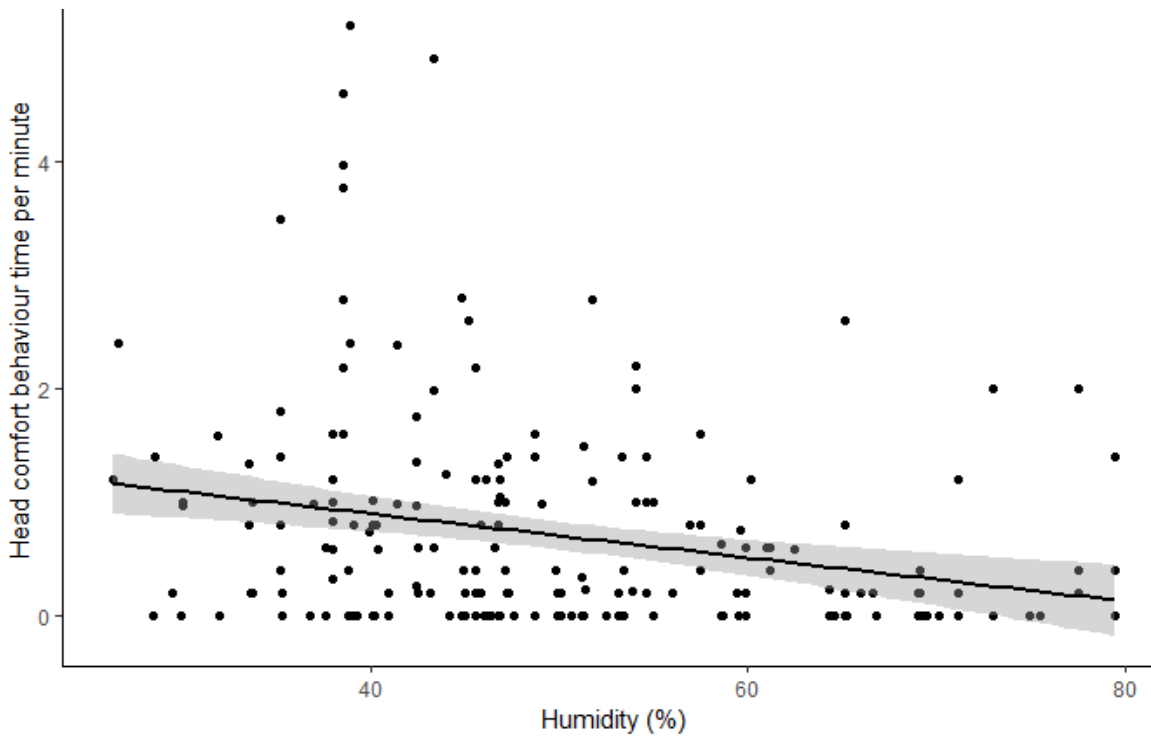


Figure 17. Scatterplot fitted with a linear regression line displaying 95% confidence intervals of air humidity and the duration of head comfort behaviours in plains zebra in Addo Elephant National Park.

5.0 Discussion

Despite significant research interest, zebra striping remains a conundrum lacking a conclusive answer. The weight of recent research has added strength to the ectoparasite hypothesis, although this still fails to conclusively separate it from the alternatives. It is known from comparing striped and non-striped equids (Caro et al, 2019), that ectoparasitic biting flies land less successfully on the surfaces of striped animals as was previously hypothesised and demonstrated in an experimental setup (Waage, 1981). However, the link between this and a lower ectoparasite load, and therefore the associated fitness advantages has not been shown, although the impacts of ectoparasites have been shown extensively (see section 2.5 “The ectoparasite hypothesis”). This study aimed to provide more conclusive data using behavioural observation of a wild population. Although comfort behaviours have previously been utilised as a proxy of ectoparasite load and the associated costs in equids (King and Gurnell, 2010) and to explore their effectiveness in deterring and dislodging biting flies (Caro et al., 2019), this is the first study to utilise this approach on a large wild population of plains zebra. This study also utilised measures of behaviour that were novel (bar the overlap of use several behaviours by Caro et al., 2019) to this field by measured both frequency and duration of each incidence of activity which had not been used in conjunction before.

5.1 Striping in the population

The quantification of striping has not been carried out on the scale of this study before (n = 625 unique individuals, Table 2), providing a fascinating and unique insight into striping across the population. The average total body striping of individuals within the population and the ectoparasite subset was the same (Figure 4). However, in neck, torso, and rump striping, a high proportion of animals had low or zero stripe scores evidencing the prevalence of quagga-like features of reduced striping (Figure 6). The Addo population also shows high rates of shadow striping (Figure 7). These features likely result from the introduction of selectively bred individuals into Addo from the Quagga Project (Harley et al., 2009). This may be evidence of selective breeding within the population towards less stripy pelage to match that of the quagga (*E. quagga quagga*), which historically was the most common equid in the southern region of Africa (Lowenstein and Ryder, 1984). The quagga has been shown, through genetic analysis, to have diverged from the plains zebra around the time of the penultimate glacial maximum ~140,000 YBP (Nehme et al., 2018), demonstrating a rapid loss of stripes on an evolutionary timescale (Leonard et al., 2005). These findings suggest that the cause of the reduced striping in the pelage of this subspecies was dependent upon conditions specific to the region. In the context of the results of this study, this would suggest the observed climatic conditions, primarily temperature and humidity coupled with wind speeds, provide ideal conditions for high ectoparasite burdens.

On a population level, the high rates of low or zero stripe counts in some body sections, mainly the rump and hindleg, represent the bulk of the animals within the park with the stripier outliers representing the direction in which the populations striping is gradually changing. However, no comparable data - from a population that had not experienced

releases or the same population over time - is available to determine whether there are differences in these features.

In both the adult population and the ectoparasite sub-sample, striping varied significantly with age and sex (see section 4.2) with juveniles having a greater number of stripes than adults (Figure 5). Some juveniles were observed to have more dark pigmentation, filling in areas between stripes that would become white over time as the degradation of pigmentation continued into the postnatal period (Prothero and Schoch, 2003). It seems most likely that this is an aberrant trait and not an indication that the increased relative surface area of dark pigmentation may afford offspring an advantage at a young age as survival strategies do not vary with age in zebra (Kingdon, 1984; Fischhoff et al., 2007). The sample size of juveniles ($n = 85$) and adults ($n=540$) was sufficient to validate any conclusions drawn from these results. Additionally, it was found that stripe counts were strongly correlated across both sides of the body in both adults and juveniles. This suggests that there is a degree of symmetry in stripe counts across the body, although this is not necessarily indicative of morphological symmetry, as patterning and morphology of striping is not accounted for in the method of quantification used.

It should be reiterated that there is a distinct lack of effect of stripe number on behavioural measures as would be expected considering the hypothesis on which this study is based, along with the wealth of previous research suggesting this would be the case. It may be that the use of stripe counts was not an effective solution for relating striping to the measured behaviours and so ectoparasite burdens. This could be seen to be a result of difference in how the human eye perceives colour compared to the ectoparasitic species considered in this study. There is a basis for arguing that the difference in eye structure and how images are relayed and processed are so great that merely counting stripes is insufficient. However, stripes must be quantified in some way and previous research uses similar if not coarser methods than in this study, often featuring broad categories or estimates rather than full detailed counts (Waage, 1981; Gurnell, 2010; Larison et al., 2015).

That there is a lack of a relationship between the measures of striping used in this study and comfort behaviours does not rule out that striping may play a role here. The morphology of striping is problematic to measure in the field due to its complexity, the movement of animals, and variation in distance and position from the observer. This area of study lends itself to analysis using statistical or GIS software where the size and shape of animals can be standardised through the manipulation of images. Stripe morphology data from a large sample such as in this study would provide interesting insights into its effect on ectoparasitism from biting flies should morphology be quantified appropriately. This would most likely entail investigating the effects of total areas of black and white pigmentation across the whole body and in individual regions of the body such as limbs or head as well as the effect of different recurring patterns. Furthermore, for a study to focus on stripe morphology as a factor in its analysis the visual cues that prevent flies from landing such as stripe orientation, size and shape must each be considered.

5.2 Predictors of striping and the effect of environmental variables

That environmental variables should be found to be the strongest predictors of behavioural differences between individuals (Table 6) is not unexpected, with temperature, humidity, and wind speed having been previously shown to drive ectoparasite activity (Herczeg et al., 2015). This is consistent with the positive effect of temperature on head comfort behaviours found in this study (Figure 16) and the negative trend of humidity (Figure 17) agreeing the effects of temperature and humidity on ectoparasite abundance and activity found in the literature (Herczeg et al., 2015), through the changes in irritation of the host species. The small effect sizes of temperature ($\beta = 0.06$, 0.03 to 0.08, Table 6) and humidity ($\beta = -0.02$, -0.03 to -0.01, Table 6) may be a result of the specific nature of head comfort behaviour as a response to irritation in a localised area, rather than its lack of importance in deterring or dislodging ectoparasites as it has been shown to be effective in this role (Caro et al., 2019).

However, temperature variation did not predict either tail swishing or full body comfort behaviours. This suggests that, although fluctuations in air temperature during sampling were large (18.5°C to 41.3°C), other environmental factors may be more important in governing ectoparasite activity at a finer scale. Neck striping was also a positive predictor of this behaviour (Table 6) although both head and total body stripe counts were poor predictors and showed non-significant trends (Figures 8 and 9).

The small effect sizes involved in head comfort behaviours are highlighted when compared with more generalist behaviours with a larger footprint across the animal's body. Tail swishing, for example, was negatively affected by increases in wind speed ($\beta = -1.62$, -2.86 to -0.39) and humidity ($\beta = -0.47$, -0.68 to -0.25) (Table 6). This behaviour also showed negative trends with total body striping, wind speed, and humidity (Figure 11, 12, and 13). Additionally, full body comfort was also strongly negatively predicted by wind speed ($\beta = -1.74$, -3.13 to -0.34) and humidity ($\beta = -0.48$, -0.71 to -0.25) (Table 6). This suite of behaviours was also shown to increase non-significantly with total body striping (Figure 10), and to decrease non-significantly with wind speed (Figure 14) and significantly with air humidity (Figure 15). Tail swishing was, in this study, the most frequent behaviour and represents the bulk of observations in the full body behaviour category (Table 4). This observation is expected from the work of Caro et al. (2019) where zebra performed this behaviour over twice as often as domestic horses under the same conditions. However, whilst this behaviour is repeatedly considered to be a comfort behaviour relevant to ectoparasites (King and Gurnell, 2010; Caro et al., 2019), it was one of the least effective in dislodging biting flies (Caro et al., 2019). Though, this was done in a temperate environment the relative rates of behaviours are similar suggesting the results are transferable. Therefore, it may be more relevant in another process such as generating airflow for thermoregulation (Wheeler, 1991; 1992). Alternatively, or possibly alongside these processes, tail swishing may play a role in signalling conspecifics although there is no evidence in the literature for this.

To summarise, the strong role played by environmental factors in the occurrence of the measured behaviours can be explained broadly in two ways. Firstly, these variables could be driving ectoparasite burdens on zebra either through changes in the abundances, species

compositions, or activity level at which each ectoparasite functions. This is evidenced in the body of research demonstrating that different invertebrate species within the same habitat have some overlap in tolerances, but ultimately optimum conditions vary between species and genus leading to some outcompeting others dependent on conditions (Sebastián et al., 2008; Waage and Davies, 1986). Alternatively, the behaviours measured in this study may have more relevance as a response to thermoregulation. And whilst temperature alone was not found to be responsible for behavioural variation, it has been shown repeatedly that both humidity and wind speed also play a major role in the uptake of environmental heat by mammals (Wheeler, 1991; 1992), in conjunction with other thermoregulatory responses such as adjustments to perspiration and respiration (Cheuvront et al., 2004). Ultimately it is therefore likely that the recorded environmental variables are confounding the results by impacting ectoparasite activity and ectoparasite comfort behaviour simultaneously though this was expected and accounted for in the analysis.

5.3 Comfort behaviours and their use as a proxy

The comfort behaviours used in this study have been shown by Caro et al. (2019), who used a similar suite of behaviours, to be direct responses to ectoparasite landings and feeding attempts. The behaviours used in this study were different to those previously used by both accounting for frequency and total duration as well as originally recording a much greater number of behaviours and then refining these down to analyse the most important. This study produced results contrary to the findings of Caro et al. (2019), with increased striping (Figure 8, 9, and 10) expressing increasing trends in behavioural activity, conflicting with the vast body of research showing increased striping should negatively affect comfort behaviour (Waage, 1981; Egri et al., 2012; Blahó et al., 2013). From this, the results could be interpreted to indicate that comfort behaviours are a poor proxy for ectoparasite burdens in plains zebra. However, the recent work of Caro et al (2019) demonstrated the direct relationship and effectiveness of an almost identical suite of behaviours to those used in this study, with walking/running included as additional comfort behaviours. It can therefore be concluded that this is very unlikely to be the case.

Alternatively, it may be that the root of this puzzle lies in the variation of the irritation thresholds of different individuals, this being the point at which a behavioural response is triggered in the host. However, previous studies validate the use of ectoparasite comfort behaviours as a proxy in plains zebra and other equid species (Caro et al, 2019; King and Gurnell, 2010). This issue would be expected to originate from a small sample size, however the distributions of each behaviour suggests that the sample size in this study would be large enough to account for this (n = 238, Table 2).

Additionally, the strong effect sizes of environmental variables in the best performing models (Table 6) may show that the comfort behaviours in Addo are instead triggered by overheating or some other form of discomfort resulting from the local climatic conditions as similar behaviours have been shown in a range of mammals (Terrien et al., 2011) where such movements are a more efficient option for thermoregulation than relying on autonomic responses. This demonstrates that whilst proxies present a valuable option when a variable cannot be measured directly, they do have inherent vulnerabilities to factors

outside those of interest, an issue discussed at length in various fields including ecology (Stephens et al., 2014), climate science (Lotter, 2003), and economics (Dechow et al., 2010). However, it seems most likely from the results of this study along with the previously mentioned research (Herczeg et al., 2015) that the recorded environmental variables are instead having a strong impact on ectoparasite abundance and activity. To determine whether this was the case, a structured survey of the abundance of various species assemblages would need to be conducted, as was planned in this study. However, in this case the unfortunate loss of invertebrate sampling equipment in the field prevented the collection of usable data to directly link comfort behaviours with ectoparasite abundance.

An unexpected finding was the seemingly small role of light intensity, time of day, and group size in behavioural activities. A large body of previous research points to these factors having a strong impact on ectoparasite activity, and suggests that they should have influenced the occurrence of comfort behaviours (Wolfe and Peterson, 1960; Allan and Day, 1987).

5.4 Conclusions and suggestions for further research

The results of this study conflict with the findings of previous research into the ectoparasite hypothesis driving zebra striping, where the negative relationship between striping and ectoparasite burdens has been demonstrated repeatedly (Waage, 1981; Caro et al., 2015; Larison et al., 2015; Caro et al., 2019). As this is the first study to quantify striping across the whole of such a large population, it seems counterintuitive that such a large sample relative to previous studies would provide conflicting results. It may be that the prevalence of comfort behaviours in plains zebra, whilst indicative of irritation (Caro et al., 2019), cannot be used reliably as a proxy for ectoparasite burdens in this case without additional information. This would require further research to accurately quantify the relationship between ectoparasite burdens and the intensity of comfort behaviours. A key part of building on this research would be, as mentioned, a structured survey of ectoparasite species and their abundance throughout the sampling period. This would need to include successive censusing of the population, which would also provide greater insight into possible changes in striping in the population and the level at which fluctuations in ectoparasite population and behavioural activity are related over that period. Further to this, the inclusion of aspects of other hypotheses in a broader simultaneous study such as predation, thermal readings, and social interactions seems likely to provide the best results as the possibility of a multi-hypothesis explanation seems to be increasing in likelihood as the long running and mercurial nature of this question evolutionary conundrum continues with no single explanation gaining traction.

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