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Award date: 2020

Awarding institution: Bangor University

Link to publication

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# The Origin of Zebra Stripes: Does Striping Provide a Fecundity Advantage?



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## Abstract:

Variety in the colouration of animals is widespread but the mechanisms that drive differences in colouration are poorly understood. The zebras' stripes are perhaps the most recognisable example of stark colouration in mammals. The evolutionary origin of stripes has been an area of contention among scientists for over 100 years. Most recent work has supported the claim that stripes aid resistance to ectoparasitic attack, but these studies have left unresolved questions with no previous study testing for differences in striping between demographic group in a population. Sexual selection systems where both sexes are ornamented are in their infancy of being understood in ecology. This study addresses one of the earliest theories for the evolution of zebra stripes, sexual selection and to ascertain whether the degree of striping of individuals is related to greater fecundity. The population of plains zebra (Equus quagga) in Addo Elephant National Park were studied for a period of 58 days commencing in January 2018. High quality imagery was taken of individuals for identification and stripe scoring of body sections. The demography of harems and environmental variables were recorded and tested against stripe scores for interactions in a range of statistical models. Differences in striping between ages, sexes, reproductive status, dominance and group type were tested for. The degree of striping of stallions and harem members had no impact on the composition and size of harems or reproductive success. Differences in striping between sexes and ages were observed and presents possible evidence of a normalising selection pressure within this population. Further investigation into the differences in striping between ages and group types across populations would be beneficial in understanding the biological relevance of these findings.

# Introduction:

The distinctive monochrome striping of the zebra is synonymous with much of Africa. The driving forces behind the evolution of this striped patterning are not, however, fully understood. There are three extant species of zebra: plains, mountain and Grevy's (Equus quagga, E. zebra and E. grevyii respectively), all of which display a high degree of striping that varies between species. Grevy's zebra are notable for their high frequency of striping but also their plain white underbelly (Caro, 2016). Mountain zebra are intermediately striped and also retain a white underbelly; uniquely they possess a prominent dewlap (Klingel, 1971). The plains zebra features the lowest level of striping, but the stripes extend the whole way around the torso (Caro, 2016). The quagga is an extinct phenotypic version of the plains zebra that was partially stripeless (Harley et al., 2009). Given that there are differences between these species ecologically, socially, and in their degree of striping, it is reasonable to assume that their stripes are derived from an evolutionary pressure or pressures that are both linked but also subtly different. The alternative being that the extant zebra species share a common ancestor which developed stripes and since then these species have evolved independently without selective pressure to lose stripes. This work will focus on the most ubiquitous and widespread plains zebra (Bauer et al., 1994).

The question as to the origin of zebra stripes was likely first raised by Charles Darwin and Alfred Russel Wallace (Darwin, 1871; Wallace, 1867). Both of these men were interested in the subject, but both took differing stances. Darwin argued that, as with peacocks, there was likely a sexual selection pressure involved while Wallace believed that stripes give animals a camouflaging advantage in low light conditions around dawn and dusk. Since then more work has been conducted on the subject and four broad hypotheses for the evolution of zebra stripes have arisen (Caro et al., 2014). These include: striping as a form of crypsis (Thayer,

1909) or striping dazzling predators or by other means reducing the chance of predation by partially inhibiting predator's ability to successfully make kills (Morris, 1990); increasing thermal efficiency of the animal under excessive thermal load through the creation of air pressure differentials along the animals' coat effectively producing a cooling breeze (Larison et al., 2015); reducing ectoparasitic attack by disrupting parasite preference for targeting more strongly striped animals (Caro et al., 2014; Waage, 1981); and that there is social and sexually selected pressure whereby striping may be used as a marker for identification, selection and dominance (Caro et al., 2014; Kingdon, 1984; Ruxton, 2002).

To date, the most studied of these hypotheses concerns that of ectoparasitic resistance, which has generated the most support, both in numerous field experiments and through computer modelling approaches (Caro, 2016; Blaho et al., 2013; Brady & Shereni, 1988; Egri et al., 2012). However, almost no work has been conducted on free roaming wild individuals or populations. Despite the limitations in research effort, there has been at least a theoretical critique of the four hypotheses (Cloudsley-Thompson, 1984; Kingdon, 1984; 2009; Larison et al., 2015; Morris, 1990).

Very little work has addressed the question from Darwin's original proposition that sexual selection may be involved. This is logical, as dimorphism of the sexes, which is commonly exhibited among ungulates, in not immediately apparent in plains zebra. However, adolescent female zebra are competed over once they begin to reach sexual maturity (Klingel, 1971). Male competition may involve physical conflict but can equally involve displays of fitness such as song in birds or heightened ornamentation of either sex (Anderson, 1996). The adolescent female is then oddly described as choosing a harem to join, rather than being forced into one or the other (Klingel, 1971; Smuts, 1976). One factor influencing this choosiness in females may be the pelage of the competing stallions or that of the wider harem through flagging of

some desirable trait. As striping bears little obvious cost it may be that stripes act as a marker of genetic compatibility as with the major histocompatibility complex (MHC) in several other species; including laboratory mice (*Mus musculus*) (Roberts & Gosling, 2003) and sticklebacks (Gasterosteus aculeatus) (Reusch et al., 2001). Sexual selection without significant dimorphism between sexes is a field of growing research in ecology and has been identified for several species (Lyon & Montgomerie, 2012; Montgomerie & Lyon, 2012; West-Eberhard, 1983). Most of this work has concerned avifauna, primates, insects and fish. The mechanisms for this from of sexual selection are most often argued to be mutualistic flagging of social status/dominance and female competition to access of mates of comparable levels to that of male completion (Montgomerie & Lyon, 2012). The result is ornamentation or adaptation reflecting choosiness in both sexes (Jennions & Petrie, 1997; Johnstone et al., 1996). In mammals especially, this requires complex social systems and the ability to live in relatively stable groups (Montgomerie & Lyon, 2012). Both of these criteria are fulfilled by the plains zebra (Klingel, 1971). The case tested here is that both males and females are competing with conspecifics to enhance their fecundity through mating with preferred partners, which is itself directed by striping. Furthermore, this selection will be reflected in greater fecundity for individuals or harems with higher levels of striping. Striping has been suggested to perform a highly social function as well as provide numerous adaptive benefits including resistance from ectoparasitic attack and abatement from predation (Caro, 2016). In this way, striping may play a role in selection of partners through flagging of desirable traits in a highly social species where energy budgets are closely aligned (Jones & Ratterman, 2009).

Another form of selection where both sexes may play a part is that of inbreeding avoidance, where exaggerated traits mark kin and breeding with kin pairs are avoided (Lehmann & Perrin, 2003). In this case, zebra may avoid reproducing with similarly striped individuals, which may

be of greater importance in this species as they can reproduce all year. No work has been conducted on the possibility of a disparity of striping between sexes or between harems. Nor has any work been previously conducted investigating the possibility that striping of dominant stallions and reproducing females may be related to size of harem and reproductive success. Interestingly, if higher striping is a possible factor influencing female entrance into a harem for plains and mountain zebra the case may also be true for Grevy's where a more classical system with obvious dimorphism in body size is documented (Bauer et al., 1994). The social system of Grevy's zebra is remarkably different from plains zebra however and features a higher degree of obvious sexual selection with stallions being larger, holding down territories and often competing for access to females (Bauer et al., 1994). Grevy's zebra are notable in that they possess a greater degree of striping in terms of frequency than that of the other two species (Klingel, 1971). This may suggest a possible sexually driven contributor to high levels of striping in this species. In this case, however, one would expect runaway selection for stripes. Alternatively, animals may be selecting individuals with which to breed based not on maximum striping but to an optimal level, thus imposing a normalising selection within a population. A similar process occurs within the MHC framework for odours, whereby signals for optimal breeding can be carried by scent (Penn, 2002). This has been demonstrated in numerous species, including humans (Homo sapiens) (Wedekind, et al., 2005), laboratory mice (Mus musculus) (Roberts & Gosling, 2003) and sticklebacks (Gasterosteus aculeatus) (Reusch et al., 2001). Striping, in this way, could be a marker for social dominance and/or optimal compatibility that is selected for across all three species of zebra. In this way, understanding the drivers of stripes in one species is likely to reflect the common evolutionary history of all extant zebra species.

It is for these reasons that this research focused predominantly on the social and sexual of these functional hypotheses for striping in zebra. All zebra species have relatively complex social systems, with plains and mountain zebra forming family groups/harems that are led by a dominant stallion (Klingel, 1971). It is believed that breeding only occurs between the dominant stallion and the females in oestrus within that harem (Klingel, 1974); however, no work has been undertaken regarding the levels of sneaky mating in the species which is likely to occur (Howie & Pomiankowski, 2016). Interestingly this close-knit social system has evolved due to the strikingly similar energy budgets made possible by their similar size and the female's ability to reproduce throughout the year (Neuhaus & Ruckstuhl, 2002). This is in contrast to most other large African herbivores where energy budgets cannot be synchronised due to the disparity in resource demands between sexes at different times of the year, this is due to the prevalence of body size dimorphism in these species (Georgiadis, 1985; Jarman, 1983).

In the case of this study, the possible role of sexual selection will be assessed using fecundity within harems, as a proxy of breeding success and sexual selection in Addo Elephant National Park, South Africa. In addition, this work will be the first to assess whether there are differences in striping between zebra of differing ages, sexes and social status. To this end, stripe data alongside ages, sexes, group composition and number was gathered. This will be tested at the social herd scale through measuring reproductive output against degree of striping. This work will be helpful in deducing whether striping in zebra is an adaptive trait maintained or brought about through selection, whether of a sexual nature or otherwise. Various genetic phenomena have been put forward suggesting that, from an evolutionary perspective, striping is a relict trait from a common ancestor for whom striping was more clearly advantageous due to environmental conditions or of genetic drift due to isolation of

population (Groves & Bell, 2004; Hack et al., 2002; Parsons et al., 2007). Specific hypotheses that are tested include:

- That there are significant differences in the degree of striping between sexes with males, especially stallions, possessing more stripes as a signal for sexual selection.
- That there are significant differences in striping between breeding and non-breeding males as a signal for sexual selection.
- That there are significant differences in the degree of striping of individuals in differing demographic and age categories with stallions and breeding females possessing optimal or greater striping as a signal for sexual selection and/or a fecundity benefit of stripes.
- That the degree of striping of individuals, particularly stalions but also breeding females, is related to those individual's reproductive success with greater or optimal striping being associated with greater fecundity through control of larger harems particularly with a greater ratio of females to males, a greater number of juveniles and stability in harem composition.
- That harems with greater or optimal levels of striping produce more offspring as a group benefit from higher/optimal striping as a signal for sexual selection and/or a fecundity benefit of stripes.

# Literature review:

All zebra species are known for their uniquely striped pelage. The origins of this striping is something that has baffled both scientist and the general public since Darwin and Wallace first debated the subject. It has become apparent that there are broadly four proposed adaptive mechanisms for the evolution of striping in zebra. These are: 1) striping as a form of crypsis as well as having "dazzling" properties that confuse predators or by other means reducing the chance of predation by partially inhibiting predator's ability to successfully make kills (Morris, 1990; Thayer, 1909), 2) increasing thermal efficiency of the animal under excessive thermal load through the creation of air pressure differentials along the animals coat effectively producing a cooling breeze (Larison et al., 2015), 3) reducing ectoparasitic attack by disrupting parasite ability to target more striped animals (Waage, 1981) and 4) a socially and sexually selected background whereby striping may be used as a marker for identification and dominance (Caro et al., 2014; Kingdon, 1984; Ruxton, 2002). The theories outlined above are centred on adaptive mechanisms for stripe evolution. There is, however, some debate as to whether zebra stripes are an anomaly of genetic drift in the evolution of species that display striping (Groves & Bell, 2004; Hack et al., 2002; Parsons et al., 2007).

To more completely explore the question of the origin of zebra stripes, this review will outline and detail the evidence surrounding each of these theories. Despite the abundance of theories presented, the quantity and quality of scientific work on the topic is concentrated on the fields of ectoparasite resistance and predation abatement. This is perhaps due to the relative ease of testing these theories, especially in the case of ectoparasite resistance, in an experimental style setup. This project is centred around an adaptive solution to the problem of zebra stripes, as opposed to the view that zebra stripes are an ancestral genetic relict, through filling in a key knowledge gap by addressing the question of the association of fecundity with

increased striping. This is something that has been assumed in other work without testing whether striping to a greater lesser actually impact breeding success in the species (Blaho et al., 2013; Brady & Shereni, 1988; Caro, 2016; Egri et al., 2012). No work has been conducted in this vein either experimentally or observationally on a population.

#### Adaptive Mechanisms & Genetic Relicts

There is an argument to be made that the evolution of stripes in zebra species is little more than a prolific relict of historic genetic change, most likely through genetic drift. This has not been explored in depth in scientific literature with the vast majority of work hoping to explain the existence zebra stripes simply assuming that they serve some adaptive function. Indeed, there is some work suggesting that degree of striping between species and populations may be driven by genetic drift (Groves & Bell, 2004; Hack et al., 2002). Although the absence of genetic structuring seen among populations that exhibit divergent stripe phenotypes suggests that striping has an adaptive function, rather than being the product of genetic drift (Lorenzen et al., 2008). Certainly, there is a degree of heredity in the degree of striping found on plains zebra (Parsons et al., 2007). However, more work is needed to verify the claims of either party.

#### Predation abatement:

Predation abatement is perhaps the longest running hypothesis surrounding striping in zebra. However, no studies have been conducted directly assessing the validity of the various assertions made. Instead inference has been used to test this broad hypothesis, largely with the result that predation abatement is unlikely to be a factor driving the evolution of striping; however, it would be premature to accept this view without an in-depth review of the

literature. Broadly, there are three ways that stripes are proposed to abate predation; camouflage, confusion and as a warning signal to prospective predators.

Thayer (1909), was one of the first zoologists to propose animal colouration as playing a vital adaptive role in terms of crypsis. In this work he specifically mentioned how striping can be used by creatures as a concealment against broken backgrounds (Thayer, 1909). While this may ring true for some species, there is little to indicate this is the case for zebra. Indeed, while it is widely known that patterning, including striping, are effective for crypsis, these patterns almost always match to some degree their backgrounds (Allen et al., 2011; Barnett et al., 2017; Godfrey et al., 1987; Karpestam et al., 2014; Karpestam et al., 2018; Kjernsmo & Merilaita, 2012). This cannot be said to be true in the case of zebra.

Nevertheless, there have been a suite of studies conducted on the ability of humans to track and target striped versus unstriped objects (both moving and stationary) against a variety of backgrounds in computerised lab simulations (Scott-Samuel et al., 2011; Stevens et al., 2008; Stevens et al., 2011). All three of these studies concluded that striping made it more difficult for a human observer to target moving objects, suggesting a possible dazzling effect of striping in motion. Despite the promising findings of these studies, they all use human proxies for predators not taking into account how different animals, particularly those likely to predate zebra, perceive the world.

How et al. (2014) built upon much of this work and developed a simulation algorithm for the kind of striping found on zebra while in motion. This work concluded that striping of a similar kind found on zebra was effective in producing a number of well-known visually impairing effects such as the wagon-wheel effect and the barber-pole illusion, especially when a pair or more individuals are moving against one another, as is the case for individual members of a herd of zebra in flight from a predator. Both effects have been linked to interfering with the

ability of individuals to accurately target moving objects, through flooding the observer's visual systems with erroneous signals (Hildreth and Koch, 1987). To date, however, no work has been conducted on zebra themselves regarding the possible anti-predator effects of striping in this fashion. Furthermore, two particularly damning arguments have been presented against zebra stripes abating predation.

Firstly, if striping were such an effective anti-predation mechanism why has this not evolved more extensively in other prey species, especially other ungulates? Indeed, even among equids striping is present to a varying degree on all of the seven extant species in this genus, but only on the three species of zebra are stripes exhibited so noticeably (Groves & Bell, 2004). Secondly, if striping were an effective deterrent from predation one would expect to observe low levels of zebra featuring in the diet of their primary predator species. However, Kingdon (1984), recorded figures for predation events on zebra from lions (Panthera leo) and found that they predated zebra at least as frequently or even preferentially to other available prey species. Hayward and Kerley (2005), supported this in their detailed work on the prey preferences of the lion. Their results concluded that lions capture and kill zebra in significantly greater proportions to their abundance, suggesting that if striping influenced a predator's ability to kill a zebra it is negligible or non-existent. It is important to note here, that this work was uncontrolled and there is no evidence to suggest that without stripes lions would predate zebra even more frequently. Furthermore, it has been recently shown that the presence of lions may affect energy budgets and time allocation in acquiring resources in plains zebra (Periquet et al., 2017) suggesting that plains zebra initiate significant anti-predation behaviour in a similar fashion to other species. In this case, stripes might be argued to be having little impact in terms of a landscape of fear induced by the presence of predators. Interestingly, this

study found significant effects of seasonality on the strength of these relationships, while also reporting no difference in group sizes of plains zebra regardless of the presence of lions.

However, in his work on spotted hyena (*Crocuta crocuta*), fewer than expected incidents of predation on zebra species occurred than expected (Hayward, 2006). This may suggest that striping is an effective means of abating predation for certain species over others. This is perhaps linked to the angle at which the stripes are viewed, as hyena are significantly smaller than lions. However, no work has tested this and spotted hyena do prefer other prey species (Hayward, 2006); to what extent striping may or may not be involved here is unknown. Despite lion's preference for zebra as a prey species one must be careful in suggesting that stripes are not still impacting their ability to predate zebra. Given that there are almost no stripeless zebra available for lions to predate upon, we cannot conclude with certainty that the presence of striping on zebra is not in fact acting as means of predation abatement; other characteristics unrelated to striping of the species may make the plains zebra easier to predate for lions over other species.

There is also a school of thought suggesting that striping may have evolved in response to a habitat background that was once widespread in Africa, mixed woodland, and was once favoured by zebra species (DeMenocal, 2004). The historic range and origin of plains zebra is complicated, however the likely first occurrence of a recognisable zebra species is believed to have occurred in Southern Africa (Pedersen et al., 2018). While not directly impinging on a predator's ability to kill a zebra, striping may have been more useful in the context of crypsis diminishing the detection probability of zebra by predators. This theory suggests that the range of this habitat has been greatly diminished and hence an obvious evolutionary driver of striping now eludes us. Thayer (1909), first developed this theory for a range of patterning and fauna and suggested that striping may be an effective camouflage in a woodland setting. For

instance, a number of adult artiodactyls exhibit striping and tend to prefer wooded habitats (Stoner et al., 2003). This has not been empirically tested for zebra but has received some theoretical attention. Furthermore, it would seem logical that if striping arose in response to a now severely diminished biotic factor then one would expect a diminishing rate of striping in zebra over time if stripes constituted a significant cost in terms of survival. Of course, if striping were cost neutral then little change would be expected.

Caro (et al., 2014), who quantified striping and modelled it against a range of variables, found no association of striping at the species level with a woodland background, although at the sub-species level there was a marginal association. However, they asserted that this was more likely due to the strong association between woodland habitats and tsetse flies (Glossina *morsitans morsitans*) rather than a form of crypsis; while further pointing out that zebra species tend to prefer open grassland. Crypsis against a savannah grassland background was addressed by Godfrey et al. (1987). They simply asserted that striping in zebra was conspicuous against a grassland background versus species like the tiger (Panthera tigris spp.). This was done by analysing the spatial frequency of stripe patterns and relating that to the chances of a similar frequency occurring as part of a natural background. This was the case for tigers but not for zebra. These results have not been replicated, however, and the methods could be updated to better understand the effect of striping in this way. Testing this by incorporating temporal variation would be helpful given that the amount and quality of the natural light varies over the course of a 24-hour period and throughout the year. While striping is highly conspicuous at midday, perhaps it provides crypsis benefits versus solid colouration at crepuscular phases when predators are most active (Mills & Biggs, 1993; Mills & Harvey, 2000; Schaller, 1972; Stuart & Stuart, 2000). Indeed, this was first proposed by Wallace (1867) and is yet to be rigorously tested. Lions are better able to predate plains zebra

under low moonlight conditions (Funston et al., 2001). However, this may be due to zebra's ability to better detect lions in the presence of moonlight rather than any effect of stripes. Plains zebra vigilance is highest during the crepuscular periods, likely in response to heightened predator activity, suggesting that stripes may be an ineffective camouflage at these times (Simpson et al., 2012). Furthermore, predation pressure has been shown to be an effective means of controlling plains zebra numbers throughout numerous managed areas (Grange et al., 2015).

In his book, Caro (2016) tested whether stripes are an effective concealant by asking volunteers whether they could perceive zebra versus other similarly sized fauna at varying stages of dawn and dusk with no significant result. Further to this he asserts that most African predators possess bichromatic vision thus nullifying the proposed effect of stipes as a camoflage. This aspect predates vision goes some way to negating all proposed means of predation abatement of stripes. Nevertheless, Caro (2016) also tested whether stripes acted as a warming signal to predators or as a means of confusion. In the first instance he proposes that most aposematic are slow and/or noisy. Caro tested how noisy zebra are through measuring noise given off by groups of zebra relative to other species. Zebra were found to be noisy but not the nosiest of species. Lastly, Caro tested whether stripes confuse one's ability to track individuals by approaching groups of zebra until they fled while taking notes on confusion. He was not able to discern a confusing effect of stripes. While these methods are somewhat unorthodox, they lend more wight against the argument that stripes are effective at abating predation.

Nevertheless, there are still questions to be answered for predation abatement hypotheses. No work has been conducted on a population of zebra and modelling work that dismiss these abatement hypotheses tend to be coarse, often not taking into account temporal or spatial

variation in habitats, different zebra species, abundance of individuals, abundance of predators and variations in striping.

#### **Thermoregulation:**

Striping as a means of better controlling body temperature versus uniform pelage colours has received significant theoretical attention but very little scientific work. Broadly, there are two schools of thought suggesting that striping may provide a thermoregulatory benefit. Firstly, that the highly contrasting nature of black and white stripes effectively produces convection currents along the surface of the dermis providing a cooling effect in extreme heat (Morris, 1990). Secondly, that striping may be effective in producing differential pressures along the hide of a zebra actively producing cooling micro-breezes (Cloudsley-Thompson, 1984). Since these suggested hypotheses little work has been conducted either experimentally or observationally to test them. This may be due to the strength of logical arguments made against them. Morris himself pointed out that the largely unstriped wild assess and the striped mountain zebra of South Africa are counter examples of stripes evolving in response to thermal load as they both inhabit very hot regions but produce few stripes. Grevy's zebra, however, inhabit more arid regions than either plains or mountain zebra and require access to water less frequently (Bauer et al., 1994). They also have particularly accentuated striping in terms of frequency of stripes. Ability to withstand lack of water may be a benefit of stripes helping to keep animals cool, but plains zebra also typically need access to water once a day (Bartlam et al., 2017). Indeed, the only paper to address the topic found no link between striping and reduced core temperatures of liquid filled barrels under varying pelage treatments where barrels were covered with the hides of pale, dark and striped cattle and zebra hides with exposure to the natural environment (Horvath et al., 2018).

However, more recent modelling studies have shown some support for temperature predicting the extent of striping in equids with a high degree of accuracy. Larison. (et al., 2014) found temperature was the strongest predictive factor out of 29 environmental factors for degree of striping, not in terms of presence or absence but extent on individuals of plains zebra. The modelling was reasonably robust, however, the authors themselves point out that the findings were not conclusive. They concluded that given the complexity of the subject, the evolution of striping is probably multifarious, combing a suite of selective factors.

Conclusions drawn about the associations found here are largely inferential and there is no evidence to suggest that individual zebra with more stripes are capable of better controlling their thermal load. Indeed, temperature is a factor that is of importance to a range of potential drivers for striping, not least the presence and abundance of biting flies. Although this was included in the work by Larison (et al., 2014) and was not found to be a significant factor. Striping as a form of ectoparasitic resistance has received much attention in its own right and will be explored in the next section.

Recently the fields of material science and engineering have taken note of the possible cooling effects of stripes. Shon (et al., 2017) measure the cooling effect of uniformly coloured versus striped panels and found that vertical stripes were optimal for cooling along the surface of striped objects, lending some idea to the plausibility of stripes aiding thermoregulation in zebra perhaps unrelated to that of core temperature. Conversely, Horvath (et al., 2018) conducted an experiment in which barrels were covered in a gradient of uniform pigments from light to dark, including striped, and measured the core temperature increase within the barrels when exposed to sunlight. They found no significant cooling effect of striped treatments. Both of these studies are fairly coarse and do not take into account any other form of cooling than a general kind; the redistribution of heat away from vulnerable body

sections may cool specific areas but lead to no net drop in temperature overall.

#### Ectoparasitic resistance:

Striping may act as a deterrent to certain species of biting flies, notably tabanids and glossinids, both genera of fly capable of transmitting deadly diseases to equids but also directly taking blood from the animal. Stripes may interfere with polarotaxis in the flies or make zebra indistinguishable from their background or more generically undesirable (Harris, 1930). These theories have attracted significant attention from the scientists and as a result there have been several studies exploring the idea, both in the form of laboratory experiments and field studies; although to date there has been no work conducted to test this on a wild population of zebra.

Waage (1981) was the first to rigorously test the effect of zebra stripes on the landing rates of tabanid and glossinid flies. Roughly anatomically correct models of zebra were set up in a field experiment and landing rates of biting flies were recorded. Black white and striped models were used as well as uniformly dark and uniformly light colours, a movement treatment was also applied. The results showed a significant preference for flies to land on dark models, with white models featuring intermediate landing rates and striped models the fewest. This experiment was later repeated with the addition of olfactory cues applied to models to better understand the role of scent in the ability of biting flies to land on a zebra. This resulted in a reduction of any effects previously shown to the point where no significant effect of landing rates between models was found. Furthermore, it would be reasonable to suggest that the addition of a grey model would have been beneficial in the work in helping to establish whether it was striping itself that was less appealing to flies not simply a mixture of black and white. In addition, he chose to only use stripes at a relative 45<sup>0</sup> angle. Adding additional angled

treatments may also have been beneficial as this has been shown to be of importance for parasitic fly targeting (Doku & Brady, 1989). Nevertheless, this work has since been built upon and largely supported in a range of similar studies.

Gibson (1992) refined the work of Waage via the addition of grey targets and both vertical and horizontal stripe treatments. This work concluded that there was no difference in the attractiveness of grey and vertically striped targets when paired together, but when the addition of black and white targets was made grey targets were as attractive as black and white ones. This suggests that the difference observed between grey and vertically striped targets is at least in part and effect of their pairing in this treatment. Horizontally stiped targets were consistently the least attractive to flies. The results of this work provide compelling evidence that flies of the genus *glossinia* are deterred from landing on horizontally stiped objects even in the presence of replicated host odours, with significantly fewer flies landing on striped host models. This work was largely repeated and supported by Blaho (et al., 2013). Vertical striping, however, was shown to have no effect on landing rates in this study. This was reasoned to be because glossinid flies prefer to use vertical planes in differentiating objects from a background, hence they are ineffective in defeating fly polarotaxis (Torr, 1989). Whereas horizontal stripes would be perceived as background effective making a zebra indistinguishable from the world. Both of these effects may be exacerbated when targets are in motion due the conspicuous movement of vertical stripes versus horizontal stripes when viewed from a horizontal plane.

Brady and Shereni (1988) also tested the effect of striping on *glossinia* landing responses. However, this work was conducted in the laboratory. This has the benefit of better controlling for potentially confounding variables that may be impossible to control or account for in field studies. However, this method lacks the validity of such field studies that may provide a more

realistic context. In this case, the landing preferences of *Glossina morsitans morsitans* and *Stomoxys calcitrans* were measured in a two-choice situation featuring black, white and striped targets. For striped targets, degrees of variation from vertical for striping was also tested. The results showed that glossinid flies preferred landing on darker backgrounds and vertical black stripes, thus supporting the idea that horizontal striping may act as an effective deterrent to landing glossinid flies for zebra.

Since these earlier studies, more recent work has refined techniques and found significant support for stripes acting as a landing deterrent to biting flies. Egri (et al., 2012) largely repeated the work of Gibson (1992), setting up experimental horse models with white, black, grey, brown and striped patterns on equid models in a horse farm in Hungary. However, this work didn't account for the effect of odour other than the presumably attractive scent of the horse farm. Notably, they also tested the mechanism by which stripes are believed to act as a deterrent; through manipulating the polarisation modulation of striped treatments. Horsefly species are attracted to polarised light (Horvath, 2008) and a high degree of variance in the nature of the polarized light reflected from a striped pattern significantly affected the landing rates of tabanids, in this case through a dramatic reduction (Lyons & Goldstien, 2018)

Caro (et al., 2014) provided further support for the ectoparasite resistance theory but from a different perspective to previous work. They attempted to model striping against a range of biotic and abiotic factors. In this case, they quantified striping from images of zebra across Africa and modelled this against a range of possible driving factors. This work concluded that there is strong support for ectoparasite resistance driving striping in zebra. However, many of the factors modelled were covariates for one another. It is for this reason that Caro did not present these findings as definitive but suggested that ectoparasites as drivers for striping is the most supported theory to date. In this assertion he is correct, however there are still

issues with the evidence presented. In the case of this study, the range and distribution of horseflies was estimated in the models from environmental factors the authors estimated to be favourable for these species of fly. Furthermore, given that almost all large African herbivores are susceptible to high parasite loads from flies (Junker et al., 2015) it is strange that striping has not evolved as a more widespread deterrent, unless there is a cost to striping in zebra particularly that is defeated by unusually high parasite potential. That is to say, striping may be more conspicuous to predators, increasing predation risk but reducing parasite burdens. This may only explain the evolution of stripes in zebra if ectoparasite attack is significantly more potent an evolutionary driver than the costs associated with increased predation risk. There is no evidence to support this assessment as such work has not been conducted. A study comparing rates of loss in populations between predation and parasite borne diseases across species would be useful but difficult to conduct.

Further information deficiencies need to be solved to assert that ectoparasites are driving striping in zebra. While it is commonly known that such parasites are vectors for particularly deadly diseases in zebra and other equids and that the amount of blood loss to some horsefly parasites is significant in high density scenarios, there is a lack of supporting evidence that this may represent significant fitness costs at a population level, especially for zebra (Foil, 1989; Hall et al., 1998; Krinsky, 1976;). However, parasite burdens in plains zebra have been linked to social dominance and fitness of individuals in Uganda (Fugazzola & Stancampiano, 2012). While this work focuses not on ectoparasites but rather intestinal organisms, it does highlight the potentially important role parasites can have on a species over time. There is little doubt that tabanid and glossinid flies can transmit a range of pathogens to fauna including equids (Foil, 1989; Krinsky, 1976). The mechanism by which transmitting occurs is well understood and occurs in two ways, biological and mechanical. Mechanical transmission is the process by

which contaminated blood on the mouth parts of flies being transmitted from one individual to another (Foil, 1989; Krinsky, 1976; Mulles, 2002). Biological transition occurs when the pathogen develops within the fly vector and is transmitted through mouthparts when feeding (Foil, 1989; Krinsky, 1976). The form of transmission varies between species, with tabanids and stomoxes being good vectors for mechanical transmission and mosquitoes and tsetse tending to transmit pathogen biologically (Chihota et al., 2001; Moloo et al., 2000; Turell and Knudson, 1987). Over the last decade there has been an observed emergence of disease in animal populations throughout Europe and Africa, Asia and Lantin America. It is widely believed that the extension of hospitable conditions to tabanid borne diseases is a primary cause. Specifically, equine anaemia have been reported in Europe and Asia (Maresca et al., 2012), bovine <u>besnoitiosis</u> is increasing in range in Europe (Alvarez-García et al., 2013; Jacquiet et al., 2010) and surra, a condition endemic in North Africa, the Middle-East, Asia and South-America, has recently been observed on the Canary Islands, mainland Spain and France (Desquesnes et al., 2013; Gutierrez et al., 2010).

The mechanism by which stripes defeat flies is still, however, not apparent and has come under question. Britten (et al., 2016) refuted the idea that biting flies were confounded by zebra stripes in their polarotaxis. Their work suggested that flies are capable of sensing zebra at any distance due to the fact that zebra reflect a positive polarized band that was discernible against a background of grasses and scrub, a background that zebra are likely to inhabit. Background has largely not been considered in previous work; this constitutes a shortcoming of studies supporting the ectoparasite theory. The conclusion of this study surmised that striping cannot be an effective means of defeating biting fly polarotaxis, however it continued to assert that biting flies are likely to play an important role in the evolution of the zebra's stripes. In addition, it has long been accepted that tsetse flies do not occur widely throughout

much of the present or historic range of zebra species (Green & Cosens, 1983). Clearly a greater understanding of the distribution and ecology of flies proposed to be a significant evolutionary driver for striping is needed before defence against ectoparasites can robustly be claimed to exert such an influence. Interestingly, in the field of anthropology, striped paints have been documented in African and Australian tribal cultures which may act as a means of deterring attack from horse flies (Horvath et al., 2019). Such a similar finding in broadly dissimilar areas would lend weight to the argument that stripes do indeed help ward off biting flies were this study not weak. The authors themselves emphasize that the principal reason for stripe body painting in these tribes are social and cultural. Furthermore, the observed effect on fly landing rates on painted human targets versus non-painted targets was weak with effects having to be combined to show a significant result.

### Social cohesion and sexual selection:

All zebra species, like most equids, are extremely social. However, plains and mountain zebra social system is based upon levels of group living (Klingel, 1971). Grevy's zebra do not live in stable social groups outside of mothers and foals (Klingel, 1971). Much of our understanding of the social system of zebra is down to the work of a few biologists studying either zebra specifically or African herbivores in general in the 1970's and 80's. Their work is widely cited but seldom repeated. Theories regarding a social aspect in the evolution of zebra striping have seen limited support with only theoretical attention, due largely to the complications evidencing them (Caro et al., 2014; Ireland & Ruxton, 2017; Kingdon, 1984; Ruxton, 2002). However, a range of possible specific drivers have been identified.

As with thermoregulation, there is a paucity of scientific literature testing the possible link between social cohesion and zebra striping. However, there has been some work on the

importance of social system in other equids, this will be explored here to better understand the role of social cohesion in zebra. Establishing the ability of zebra to recognise one another visually has never been tested, but work has been conducted on other equids. Lovrovich (et al., 2015) showed domestic horses (*Equues ferus*) are capable of solving three-choice tasks in a dynamic way. Hanggi & Ingersoll (2009) showed that domestic horses have complicated longterm memory. Proops (et al., 2009) and Sankey (et al., 2011) both demonstrated that domestic horses are capable of recognising both con specifics and humans. Basile (et al., 2009) went one step further and showed that horses are capable of recognising con specifics from their whinnies. From this it is clear that domestic horses are capable of recognising one another and handling relatively complex problems over time. This has not been demonstrated for any of the zebra species, but it is a reasonable assumption that they are capable of similar processes given their relatedness.

Kingdon (1984) suggests that zebra stripes may aid zebra species in facilitating higher levels of cohesiveness. This argument is centred around the unusually social nature of plains and mountain zebra. Kingdon argued that stripes aided identification, as all zebra have an individual stripe pattern that perhaps also acted as markers for grooming. Thus, stripes evolved from a social mechanism whereby survivability is higher for individuals within more socially cohesive groups and that this was linked to striping. However, there is no empirical evidence to support this. Indeed, equids are known to use a variety of methods for identifying individuals including olfactory and auditory ques (Proops et al., 2009). Cloudsley-Thompson (1984) supported the marker for grooming theory that Kingdon (1984) while also suggesting an innate socially cohesive role of striping. It was suggested that stripes aid individual recognition and reinforce inter-individual bonds in social harems. This too has no backing in the form of peer reviewed literature, instead relying on largely anecdotal accounts.

The plains zebra reproductive unit is that of the harem which is dominated by a stallion (Smuts, 1976). While socially stable bachelor groups lend a second tier to the social system of plains zebra. Occasionally, both harems and bachelor groups will join creating unstable mixed herds. There is seemingly little competition between stallions for access to females however, adolescent females are competed over once they begin to reach sexual maturity (Klingel., 1971). Male competition between existing stallions and individuals from bachelor groups can involve physical conflict but can equally involve displays of fitness such as posturing (smuts, 1976; Simpson, 2012). The adolescent female will typically choose a harem to join or be forced into the fitter stallion's harem (Klingel., 1971 & Smuts., 1976). It remains unclear as to the balance of power in this aspect of zebra life, there may well be active female choosiness over competing stallions and striping may play a role in this. However, no work has been conducted to test this. Benefits of the harem system are bilateral, and females should not be considered as passive agents in these systems (lyengar & Starks, 2008).

Striping, both in terms of extent and pattern would certainly make useful choosiness signals especially with the context of a highly social species like zebra. Furthermore, bachelor groups of plains zebra are highly stable (Fischhoff et al., 2009). What influences the formation and maintains the stability of these groups is unknown, but striping may be a factor. Relatedness may also play a role in the formation of mixed herds for plains zebra. Tong (et al., 2015) showed that females preferentially mixed with kin in herds while males showed no such preference. It is unknown to what extent related zebra share stripe frequencies and patterns, but this must be taken into account when attempting to consider stripes as important in a social context. In a study of captive plains zebra, Pluhacek (et al., 2006) found that the reproductive success of higher order (socially) females was greater than those lower down the hierarchy. Factors influencing the structure of this hierarchy are little known and stripe

patterns may have an influence if not as a traditional signal of fitness but perhaps as a marker for genetic compatibility in a similar way that MHC signalling is utilized in other species (Penn, 2002).

Sexual selection without significant body size or ornamental dimorphism between sexes is a field of growing research in ecology and has been identified for a number of species (Lyon & Montgomerie, 2012; Montgomerie & Lyon, 2012; West-Eberhard, 1983). To date the majority of this work has been concerned with avifauna, but also with mammals, insects and fish. In particular primates, including the mandrill (Mandrillus sphinx) and Chacma baboon (Papio ursinus), have females that produce ornaments involved in mating (Huchard et al., 2010; Setchell, 2016). Anecdotally, there is little difference between the pelages of male and female zebra. However, differences in body weight and size differs little between the plains zebra sexes and their respective energy budgets are very closely aligned (Hack et al., 2002; Neuhaus & Ruckstuhl, 2002). This is in contrast to most other large African herbivores where energy budgets cannot be synchronised due to the disparity in resource demands between sexes at different times of the year, the result of body size dimorphism. The mechanisms for sexual selection in the absence of dimorphism are most often proposed to involve flagging of social status, dominance and female competition of similar levels to that of competition between males (Clutton-Brock, 2007; Clutton-Brock, 2009; Hunt et al., 2009; Tobias et al., 2012). This is particularly the case for species where males invest in offspring, pay high costs in order to breed or low costs to in finding a mate, or when female quality is very variable (Johnstone et al., 1996; Kokko & Johnstone, 2002; Kokko & Monaghan, 2001). Juveniles stay with harems for considerable time and stallions play a role in protecting them (Klingel, 1971). Furthermore, competition for females is documented as being relatively sedate reducing the cost to finding a mate dramatically (Klingel, 1971). Interestingly, it is also possible that stripes may act as

signal for innate genetic compatibility through MHC signalling, this has been suggested for chacma baboons (Huchard et a., 2010). The case presented here is that both males and females are selecting conspecifics in order to enhance their fecundity through mating with preferred partners.

Striping has been suggested to perform a highly social function as well as provide numerous adaptive benefits (Caro et al., 2014; Ireland & Ruxton 2017; Knight, 2017; Ruxton, 2002). In this way striping may play a role in selection of partners through flagging of desirable traits in a highly social species (Jones & Ratterman, 2009). Interestingly, if higher striping is a possible factor influencing female entrance into a harem for plains and mountain zebra, the case may be so true for Grevy's. Their social system is remarkably different however and features a higher degree of obvious sexual selection with stallions holding down territories and often competing for access to females. Grevy's zebra are notable in that their striping is much more pronounced than that of the other two species (Klingel., 1971). This may suggest a possible sexually driven contributor to high levels of striping in this species. Striping, in this way, could be a marker for social dominance that is selected for across all three species of zebra. It is worth noting, however, that many of the referenced studies investigating zebra behaviour are both dated and unrepeated. Yet, they are highly regarded and often used as reference in other literature.

Recent work has proposed a novel social explanation for zebra stripes. Ireland & Ruxton (2017) argue that stripes may act as an interspecific species signal for mixed herding with stripes acting as a signal for herding in other ungulate species. This would provide a benefit from reduced chance of predation and possibly foraging benefits due to the differing niche that zebra occupy in terms of graze selection as hind gut fermenters (Sinclair, 1985); thus, explaining why stripes may have evolved in zebra and not more widely in other African

herbivores. This has been suggested as a possible mechanism and to date has not received any evidential support.

#### Other striped species:

It is important to note that striping in the manner of which one finds on zebra is not unique to zebra species. Indeed, within the three extant species of zebra there is also noticeable variation in stripe morphology. Grevy's zebra possess the greatest frequency of striping of any zebra species and are the largest both in body size and mass (Figure 1) (Bauer et al., 1994). They are notable as being less socially cohesive than plains or mountain zebra, living in small unstable groups (Ginsberg, 1989). Males hold down breeding territories and will defend them violently when there is competition over females. Grevy's zebra populations are limited to hotter regions of Kenya and Ethiopia (Moehlman et al., 1998).

Mountain zebra are similarly striped to plains zebra but are believed to be anecdotally intermediately striped while also retaining a plain white underbelly (Figure 1). They have a similar social system to plains zebra with highly cohesive harem based reproductive group structure (Penzhorn, 1984). They inhabit mountainous regions of Southern Africa, but recent works suggests that this trait is the result of marginal fringe populations holding on during severe population decline from a core range (Weel et al., 2015).

The wild African ass (*Equus africanus*) is limited to two populations in North East Africa and are considered to be two different subspecies; the Somali wild ass (*E. a. somaliensis*) and the Nubian wild ass (*E. a. africanus*) (Groves, 1986). Both subspecies occur above the central Sahara and inhabit very arid regions (Groves, 1986). Their social system is similar to Grevy's zebra and is not considered to be strongly socially cohesive (Marshall & Asa, 2003). As with Grevy's they live in loose and unstable groups and males are highly territorial (Marshall & Asa,

2003). Unlike the zebra species the wild asses are not heavily striped although both subspecies possess a feint ventral stripe and the Somali wild ass has black and white horizontal striping along the bottom of the legs (Figure 1).

The quagga (*Equus quagga quagga*), an extinct subspecies of plains zebra endemic to South Africa, is especially interesting in this work as the Addo Elephant National Park population of plains zebra were involved in a project that attempted to back-breed individuals to a quagga like state (Quagga project, 2005). Little is known about the quagga's ecology but they possess a half set of zebra like stripes, with the front half, neck and head being striped and the rest of the body plain (Figure 1).



Figure 1: A) Grevy's zebra. B) Mountain zebra. C) Quagga. D) African wild ass. Images from:
A) https://www.edmonton.ca/attractions\_events/edmonton\_valley\_zoo/animals/grevys-zebra.aspx
B) https://www.marwell.org.uk/conservation/action/species-listing/hartmanns-mountain-zebra
C) Frederick York (d. 1903) -

https://www.archive.org/stream/extinctanimals00lank?ref=ol#page/n49/mode/2up D) http://animalia.bio/african-wild-ass

#### Summary:

The four main hypotheses presented above have each been tested to a lesser or greater degree. 1) Striping as a form of crypsis and predation abatement has received moderate attention with no clear conclusion. There is certainly evidence that striping can produce illusions and impair the human ability to track an individual (Scott-Samuel et al., 2011; Stevens et al., 2008; Stevens et al., 2011), but no work has been produced directly assessing the proposed effects of stripes on a predator's ability to catch zebra. 2) Striping providing thermal efficiency benefits has received little attention. The work that addresses this issue is somewhat contradictory however, the recent work of Bartlam (et al., 2017) that establish no link between striping and the reduction of the core temperature of simulated zebra seems to represent the majority of opinion and is the most robust paper on the topic. 3) Resistance to ectoparasitic attack dominates the literature for zebra stripes with a good amount of support. The works of Gibson (1992), Blaho (et al., 2013) and Caro (et al., 2014) go a long way to establishing stripes as an effective deterrent to landing rates of parasitic flies. However, the exact mechanism by which this is achieved is not yet understood (Britten et al., 2016). 4) Social cohesion and sexual selection have excited the least scientific work and that which has been published has focused almost entirely on social cohesion with mixed results (Cloudsley-Thompson, 1984; Fischhoff et al., 2009; Ireland & Ruxton, 2017; Kingdon, 1984) but no work has directly considered sexual selection. The evolution of zebra stripes has left unanswered questions which need addressing before a conclusive mechanism for the evolution of stripes is agreed. More work is required on the topic to fully tackle the problem and it is hoped that this study will go some way to doing so.

## Methods:

#### Study Area:

Addo Elephant National Park (Addo) is one of South Africa's 19 national parks and is the third largest at 1,640 km<sup>2</sup>. It is located in the Eastern Cape Province, 72km north-east of Port Elizabeth. Unlike much of sub-Saharan Africa, it lacks a distinct wet and dry season with an average of 538 of precipitation falling throughout the year (Smakhtina, 1998; Schulze & Lynch, 2007). Addo hosts a large number of herbivores including ~600 plains zebra (SANP, 2016). These zebra were originally introduced as part of a selective breeding programme hoping to back-breed plains zebra to display a more quagga-like phenotype (Harley et al., 2009). As such, they constitute an ideal study population for examining the factors affecting the evolution of striping due to the extensive variation in pelage found within individuals in the park.

The park is comprised of four main sections, including a coastal and mountainous section. For this work, research was confined to the two main game sections: Main Camp and Colchester. Historically these sections were separated by game fencing, however the fences have now been removed. The density of greater kudu (*Tragelaphus* strepsiceros), African bush elephants (*Loxodonta africana*) and Cape buffalo (*Syncerus caffer*) is notably high (Gough & Kerley, 2006; SANP, 2016). Much of the park is comprised of Thicket biome, with areas of densely packed vegetation made up largely of spekboom (*Portulacaria afra*). More open areas, historically agricultural areas of grassland, proliferate particularly where elephants are most commonly active (Volk et al., 2003). There is no free-flowing natural water within the Main Camp or Colchester sections, so water is piped to designated watering holes throughout the park.

#### Materials and Methods:

Fieldwork commenced in January 2018 and proceeded for 58 days. The principal objective of the fieldwork was to capture images of both sides, heads and rumps of individual zebra. Images were captured using Canon EOS<sup>®</sup> 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 lenses. All images were captured from a vehicle on marked tracks. Upon discovery of a group, their location was taken using a Garmin Etrex<sup>®</sup> 10 model configured to UTM coordinates; time of day, distance to group and bearing from the vehicle was also recorded using a Nikon® laser reflective rangefinder and a GWHOLE® sighting compass. Distance was taken to be the centre point of a group. The habitat was also noted and separated into three coarse habitat types: grassland, scrub and thicket. This enabled testing for associations between striping and habitat type. The number of individuals of a group was identified and recorded, along with the sex of each individual, which was largely determined using the distinctly greater area and shape of dark pigmentation around the female's anus and vulva when compared with a male; obvious sex specific organs were also used when available (Figure 2). Age was recorded also and was split into two classes: adult and juvenile with juveniles being approximately  $\leq$  75% the mean size of present adults. Mothers of foals were identified through observation and confirmed when foals suckled from their mother. Pregnant females were identified from significant elongation of their abdomen on the horizontal axis and through swelling and lactation from mammary glands (Figure 3). Stallions were identified through behavioural observation and group demographics; including displays of dominance and leadership (Kingdon, 1984). The oldest male in a harem, identified by clear signs of ageing including duller coloration in pelage, signs of wear on hooves, prominent scars and a reduction in muscle tone, was usually considered the stallion. This may have been prone to inaccuracy as only a general appraisal of age can be made by these means.

This data, with stripe scores, was used to test for differences in striping between ages, sexes and groups types with the expectation that stallions with greater/optimal striping would control larger harems and that breeding females would possess greater/optimal striping. This analysis was also extended to breeding females A group type was ascribed to every group based upon numbers and demographics; these are: harem, bachelor group and mixed herd. This allowed for analyses testing for differences in striping between demographic groups with the expectation that harems would possess greater or optimal striping that other group types. Individuals identified as stallions were the only males assumed to have reproduced within a harem. Females were taken to have reproduced if they were identified as being pregnant or showing clear signs or recent foaling including suckling juveniles, swollen mammary glands and lactation. It was not possible to gather absolute paternity data as direct samples could not be taken from individuals due to limitations placed on fieldwork the SANParks authority. A measure of group striping was taken (mean) for bachelor groups and harems to test for differences between them. Harem striping was also tested against several variables including sex ratio, number of females and number of juveniles with the expectation that groups with greater or optimal mean striping would produce more offspring or have the potential to do so.



Figure 2: The posteriors of a female (left) and male (right) zebras as told by the strikingly different area of dark pigmentation around the anus and genitals.



Figure 3: A heavily pregnant female (left), differentiated by the very noticeable horizontal elongation of the abdomen when compared with non-pregnant females (right)

When a group was encountered, they were given a unique herd ID and individuals within the herd were given an individual ID that was linked to their herd. Individuals were constantly observed throughout data collection to be sure of identity. Images were taken of as many individuals in a group as possible, with right and left sides and head and rump images being taken separately. As each image was taken, the image number was noted down by a scribe and linked to the corresponding individual ID. Ageing and sexing occurred simultaneously to image capturing. Binoculars and a spotting scope were used to aid this where necessary. In the case of the discovery of a group of zebras that were at extreme range or largely hidden no images were taken and the group was not recorded. Where the identity of a zebra was confused, it was re-identified using pictures already taken. If this was not possible it was discounted from the images but remained a member of the group in total group size.

To minimise the chance of pseudoreplication, data was collected from the Main Camp and Colchester sections on alternate days with different routes being driven each consecutive day in a section. Data collection typically began when the gates to the park were opened each morning and continued until they closed at dusk, these times varied but opening times generally fell between 05:00 and 06:00 hours with closing generally falling between 17:00 and 19:00 hours. Constant surveying for groups was conducted while driving through the park. Once an area was sampled, it was not sampled again that day. The daily time spent sampling was largely dependent upon number of groups encountered but typically lasted between 4 - 8hours. Instances of injury to individual zebra or the presence of predators was noted when it occurred.

Zebra images were entered into the Stripe-Spotter software to identify individuals and quantify any duplication (Lahiri et al., 2011). It is impossible to quantify the degree of error incurred in the use of Stripe-Spotter to identify individuals and therefore inform resampling, but its performance was noted as being severely impeded by image quality and variations in lighting and the angle of images when manually checking imagery. Additionally, an initial effort was made during fieldwork to ascertain specific mother/foal pairs to undertake analyses on the potential links and differences between these individuals. This proved prohibitively
difficult in practice as most harems encountered with a foal tended to have more than one. Stripes were counted according to a modified Harley's stripe scoring method, with total black stripes being counted for 8 sections of the body (Harley et al., 2009). This method was expanded to include shadow stripes and otherwise non-standard stripes (where stripes altered direction or were erratic). These changes to the method were made to more completely incorporate stripes that would otherwise be deemed trivial. This was of importance due to the widespread variety of striping between individuals in the park, itself a product of the quagga project. This method differs from the method used by Caro (et al., 2014) and Larison (et al., 2015) significantly. In the case of Caro (et al., 2014), stripes were recorded across the belly only if they intersected the ventral stripe. Leg and shadow stripes weren't counted but were given intensity scores based on vividness and prevalence across sections. Stripes on the face and neck were counted and directions stripes on the rum and groin area were given number and intensity scores. In Larison's (et al., 2015) work, thickness and stripe saturation was recorded for all stripes and stripes were only counted if they crossed an overlaid midline on specific body sections. In this work no attempt at measuring thickness or stripe saturation was made as variation in conditions affecting induvial images was deemed impossible to standardise.

The sections included in stripe counting included: face, head, neck, torso, belly, foreleg, hindleg and rump (Figure 4). The face was taken to be any stripes contained between the eyes and as far up as the mane. The area considered to constitute the head was any stripes forward of a line drawn vertically down from the point at which the ear joins the neck. The neck was taken to be, any stripes behind the ear and to a point drawn vertically down from the haunches, as these were always easily visible, and above the pelvic joint of the foreleg. The torso was taken to be any stripes behind the neck and above the pelvic joint of the hindleg. Belly stripes are a recount of torso stripes, but only those which joined the ventral stripe on the underside of the animal. Both the foreleg and hindleg were counted from below their respective pelvic joints to their maximum extent. The rump constituted any stripes occurring significantly on the rear section of the animal. Where stripes overlapped sections, they were counted in the section where the majority of the stripe presided. Stripes were defined as: an area of dark to black pigment, surrounded by lighter to white pigment and exhibiting a distinct directionality. This being the case, stripes that were technically contiguous but differing in direction and still being surrounded by lighter pigment were counted as separate. Shadow stripes were counted separately but had to fulfil the same criteria as a stripe in order to be counted with the added criterium of being distinctly lighter in colour to their surrounding stripes. For a stripe that exhibited traits of both conventional and shadow striping its classification was determined by majority in total area that stripe best fit the definition. Separate totals for stripes and shadow stripes were derived from counts, a combined total was also derived from these counts and this was used for a final total figure of striping for

### individuals.



Figure 4: The division of the body, face and rump in line with the Harley's stripe scoring system. Regions are numbered 1 - 8 and are: head, neck, torso, belly, foreleg, hindleg, rump, face. Both the prominent stripes are counted and the less distinct shadow stripes. Shadow striping is particularly noticeable on the hind quarter of the top animal in this figure.

Mane length and tail length were ranked from each image from 0 - 3, with 0 being not present, 1 being  $\leq 25\%$  the height of the ear when vertical, 2 being  $\leq 50\%$  the height of the ear when vertical and 3 present in its entirety. The general background colour of individuals was categorised as: white, cream, light brown and dark brown for each individual. The quality of the images for the purpose of stripe scoring was ranked between 1 and 4, where 1 was all sections good (a very clear image of a zebra containing all body sections in full), 2 was all sections not good (some distortion of the image was present due to range and weather conditions, in some cases very minor areas were obscured by vegetation), 3 was up to two sections missing and 4 was greater than 2 sections missing. For the purposes of analysis, images with a score > 2 were removed.

### Analyses:

All statistical analyses and graphical plots were performed using R statistics in RStudio R (v. 3.5.3; R Foundation for Statistical Computing, Vienna, Austria). Tests for normal distribution was undertaken visually with histograms and Q-Q plots using ggplot2 package. Differences in striping between demographic types (age, sex, group type and social status) were tested using ANOVA in instances where the variables were normally distributed. Where this was not the case, a Kruskal Wallace test was performed. Correlation was used to compare striping between sides/body section for individual zebra. Within group analysis was undertaken to test for effects of individual striping of stallions with multiple variables (Table 1). Given that juveniles only occur within harems, and that harems are the semi-stable reproductive unit for plains zebra (Kingdon, 1984), the bulk of the analysis in this work was performed within harems. Analysis for harems was further limited by the necessity for good quality images for  $\geq$ 50% of the group. If this criterion was met an average stripe score was calculated per harem. Generalized linear mixed models (GLMMs) with a Poisson distribution function and a crossed random effect, unique stallion ID, were used to perform this analysis in R using the package "Ime4". The models run for this analysis are detailed below (Table 1). This analysis further included a null model (intercept only) against which models with test parameters were compared to assess model performance. Model selection using Akaike's Information Criterion

(AICc) in "AICcmodavg" was undertaken (Burnham & Anderson, 2002).The "AICc-modave" package was used to acquire AIC scores/weights for the candidate models, further model averaging was undertaken on the top models which held 95% of the AIC weight and parameter β were used to assess the relative effect sizes for the specific variables in the models. Where returned confidence intervals overlapped zero, no confident inference could be made. Stallion striping and reproductive success and group size showed a possible non-linear relationship in descriptive plots. Therefore, generalized additive models (GAMs) were performed in "mgcv" to explore these relationships. As with the GLMMs, AIC and parameter β estimates were used to discern the relative effect sizes for the specific variables in the models. Where tests for differences in striping between factor age or sex categories with non-Gaussian distributions was undertaken, a Kruskal-Wallace test was used.

Candidate Models			
Dependant Variables	Explanatory variables		
Group size Number of females Number of juveniles Total associated females Total associated juveniles Average group striping	Null Total stallion stripes Total stallion head stripes Total stallion neck stripes Total stallion torso stripes Total stallion belly stripes Total stallion legs stripes Total stallion head+neck stripes Total stallion head+neck stripes Total stallion head+neck+torso stripes Habitat Average group striping Group sex ratio (including juveniles) Group sex ration (excluding juveniles)		

Table 1: The variables included for the models run for the within harem analysis. A total of 71 models were run over 6 dependant variables. All combinations of the listed variables were tested.

# Results:

### Sampling Effort and Demographics:

Images were captured for a total of 1234 individual zebra. These images were input into the Stripe-spotter database to identify individuals and record resamples. From this, a total of 628 known individuals were identified as well as 194 unknowns. Of the 628 known individuals, 274 were associated with images with a quality of  $\geq$  2. This population was deemed suitably large to test for differences in striping between ages, sexes and group types to test for possible selection pressure/s. This level of image quality was chosen as a watershed for analysis as it provided the best resolution images for analysis. These individuals were further split into 5 group types (Figure 5).





A gender split of 147 male (53.7%), 118 female (43.1%) and 9 unknowns (3.3%) was observed within this sample. The disparity between the number of male and female zebra observed can

be explained as the product of chance due to this sample being based on image quality. A total of 237 (86.5%) individuals were recorded as adult and 37 (13.5%) as juvenile, no animals were unaged.

### Harem Sampling Effort and Demographics:

Harems underwent noticeable and underestimated flux during the sampling period; given this a harem was considered as the same group if  $\geq$  50% of the individuals within the harem remained consistent between resamples. The stallion within a harem constitutes the principal reproductive individual, thus analysis also prioritised good quality images for known stallions in order to test for associations between stripe scores and harems size, composition and stability. The within harem analysis was comprised of 62 groups, 36 of which were considered as being unique. This further corresponded to the total number of 36 unique stallion across all 62 harems. Of the 36 stallions, only 8.3% changed group, thus the majority of movement between harems was undertaken by females, subordinate males and juveniles. It is reasonable to assume that some of the changes in group composition were the result of young animals maturing and leaving the harem although this effect may be limited by the relatively short study period. This was not measured, however. Analysis was not restricted to the unique groups, however, as changes in group composition occurred within resamples altering the composition and group stripe scores for groups with the same ID. This was the result of the decision to retain a group ID when > 50% of the individuals remained consistent over time.

Average group size for harems was 5.4 (s = 2.17). Females comprised the highest proportion of individuals within harems averaging 3.4, with males and juveniles making up only 1.98 and 1.27 respectively (Figure 7).



Figure 7: The average composition of harems by sex and age, males represent 1.98 (SD = 0.93) individuals per harem, females 3.4 (SD = 1.66) individuals per harem and juveniles 1.27 (SD = 1.1) individuals per harem. Add numbers to mean

### Stripes:

Across all images of an acceptable quality for all known unique zebra, the mean total striping (excluding faces and rumps) was 196.58 (N = 265, SD = 25.26). This ranged from 123 – 261 stripes overall. The number of juveniles within this analysis was 35. Females were observed to have significantly more stripes (M=200.20, n = 147, SD=23.68) than males (M=193.67, n = 118, SD=26.17) as determined by an independent samples T-test, t(259.22)=2.12, p=0.034. A Kruskal-Wallis Test was conducted to assess potential differences in total striping between adults and juveniles due to the non-normal distribution observed for juvenile striping and striping by induvial body section. Juveniles (M=204.6, SD=21.93) were significantly more

striped than adults (M=195.36, SD=25.55)  $X^2$ =4.69(1), p=0.030. This analysis was repeated by

body section for differences in ages and sexes and is outlined in tables 2 and 3, that show the

juveniles possessed a greater number of leg stripes than were present on adults (Table 3).

Body Section	Х	SD	X <sup>2</sup>	р
Head				
8	37.88	5.94	0.036	0.84
<b>\$</b>	38.03	5.99		
Neck				
8	36.35	5.88	2.22	0.13
<b>\$</b>	37.52	5.4		
Torso				
3	38.83	6.26	4.08	0.04*
<b>P</b>	36.42	5.38		
Belly				
3	9.37	3.4	0.01	0.91
9	9.33	2.74		
Foreleg				
ð	35.22	9.87	3.53	0.06
Ŷ	37.17	9.61		
Hindleg				
3	37.25	9.89	1.83	0.17
Ŷ	38.67	9		

Table 2: The results of Kruskal-Wallis tests performed on the stripiness of individual body sections between male and female zebra. Significant values have been marked with an \*

Body Section	Х	SD	X <sup>2</sup>	р
<b>Head</b> Adult Juvenile	37.99 37.69	6.07 5.18	0.11	0.73
<b>Neck</b> Adult Juvenile	36.73 37.77	5.66 5.47	0.99	0.31
<b>Torso</b> Adult Juvenile	35.65 34.8	5.8 6.05	0.82	0.36
<b>Belly</b> Adult Juvenile	9.37 9.26	3.17 2.18	0.01	0.89
<b>Foreleg</b> Adult Juvenile	35.28 41.43	9.57 9.61	12.42	0.00*
<b>Hindleg</b> Adult Juvenile	37.43 40.86	9.67 7.92	4	0.04*

Table 3: The results of Kruskal-Wallis tests performed on the stripiness of individual body sections between adult and juvenile zebra. Significant values have been marked with an \*

As shown in tables 2 and 3, males have marginally more torso stripes than females, while juveniles are more striped across the foreleg and hindleg than adults. This analysis was repeated for known male individuals within 3 dominance categories: stallions, bachelors and subordinate males (males within a harem). No significant difference in striping was observed between these categories either in degrees of total striping or striping per body section. The higher degree of striping across juvenile leg section may indicate a selection pressure, however given the similarity in striping between stallions, bachelors, females and males these is no compelling evidence to suggest sexual selection.

A Kruskal-Wallis Test was conducted to assess potential differences in striping between females who were identified to have had a foal and those that had not due to the non-normal distribution observed for these groups. Females were taken to have reproduced both over the

study period where new young were observed and prior to the study period where they could

be identified with larger young. The results of which are detailed in table 4.

Table 4: The results of Kruskal-Wallis tests performed on the stripiness of individual body sections between females who had reproduced and females that had not. Significant values have been marked with an \*

Body Section	Х	SD	X <sup>2</sup>	р
Total				
Reproduced	183.82	27.26	4.85	0.02*
Not reproduced	197.72	24.56		
Head				
Reproduced	34.06	5.4	7.47	0.00*
Not reproduced	38.56	6.04		
Neck				
Reproduced	37.06	5.77	0.01	0.00
Not reproduced	37.26	6.34	0.01	0.90
Torso				
Reproduced	37.82	5.92	1.22	0.26
Not reproduced	36.3	6.65		
Belly				
Reproduced	8.47	2.24		
Not reproduced	9.16	2.47	0.04	0.47
Foreleg				
Reproduced	32.18	9.48	2 97	0.04*
Not reproduced	37.25	9.65	5.07	0.04
Hindleg				
Reproduced	34	8.68	4.11	0.04*
Not reproduced	38.92	9.45		
•				

As shown in table 4, females that had not reproduced had significantly more stripes both across the body as a whole and on the head, foreleg and hindleg. The expectation that greater/optimally striped individuals produce more offspring has, therefore, been shown to be false within the timeframe and confines of this study. A Kruskal-Wallis Test was conducted to test for differences in striping between stallions and bachelor males. No difference in total body striping was observed (stallions X=194.38, SD=25.37; batchers X=194, SD=24.4) X<sup>2</sup>=0.53, p=0.77. This was repeated by body section but no significant differences were observed.

## Within Harem Analysis

Of the 71 models run across all six dependant variables for this analysis, only 6 outperformed

the null model with the dependant variable mean harem striping; no model run on the five

remaining dependant variables outperformed the null (Table 5). From these, it was not

possible to establish support for a relationship between any of the variables tested (Table 6).

Values for models that failed to outperform the null model have not been given.

Table 5: The candidate models that outperformed the null model and accounted for  $\geq$  95% of the AIC weight for within harem analysis for average group striping. All models shown were for the response variable mean harem striping.

Model	К	AICCc	AICCc Weight	Log Likelihood
			C	
Group sex ratio+Total stallion striping	5	0	0.33	-221.41
Group sex ration (excluding juveniles)	4	0.46	0.26	-222.83
Group sex ration (including juveniles)	4	1.58	0.15	-223.39
Group sex ratio (including juveniles)*Total stallion striping	6	1.66	0.14	-221
Group sex ratio (excluding juveniles)*Total stallion striping	6	2.20	0.11	-221.27
Total Stallion striping	4	28.19	0.00	-236.72

Table 6: Parameter  $\beta$  estimates (± 95% confidence intervals) for the models outlined in table 3. SE for each model and variable combination overlaps zero thus no inference on relationships between these variables can be made.

Response Variable	Parameter	β estimates	95%CI
Average Harem Striping	Group sex ratio (inc. juveniles)	-4.81	-30.44, 27.03
	Group sex ratio (exc. juveniles)	13.07	-31.46, 30.11
	Total Stallion Striping	-4.16	-22.47, 29.17

Due to the possibility of a non-linear relationship between stallion striping and harem demographics shown in descriptive plots, the possibility of using GAMs was explored. The same approach was taken as with GLMMs. However, in this case no candidate model outperformed the null model. Given these results, the expectation that striping is related to either sexual selection in the form of preferential breeding between greater/optimally striped stallions/females or increased fecundity for individuals/groups in the form of a higher level of associated juveniles with more/optimally striped individuals or groups has not been satisfied. The higher greater number of stripes observed on across juvenile leg sections when compared with adults may suggest a selection pressure for striping in these regions, however this may merely be a developmental phenomenon.

# Discussion:

Striping in zebra is most believed to be the adaptive result of a selection pressure or pressures (Caro etal al., 2014; Cloudsley-Thompson, 1984; Kingdon, 1984; 2009; Larison et al., 2015; Morris, 1990). There are suggestions, however, that zebra stripes are little more than a relic of past genetic drift in the common ancestor of modern zebra species (Groves & Bell, 2004; Hack et al., 2002; Parsons et al., 2007). It is generally considered that there are three processes by which adaptive traits are maintained within a population: stabilising, disruptive and directional selection (Mousseau & Roff, 1987). Stabilizing selection acts to maintain an advantageous trait at an optimal maximum (Hanssen, 1997). Directional selection tends to push an advantageous trait toward ever more extreme values (Hoekstra et al., 2001). Disruptive selection, thought to be the most uncommon type, alters traits in more than one direction when the current state is sub-optimal (Rueffler et al., 2006). This tends to occur in transition periods and is thought to be the precursor to speciation in many cases (Martin & Pfenning, 2009). If striping in zebra is under selection, then one would expect to observe an effect of stripes on the fecundity of individuals or groups. However, no biologically relevant effect was shown in this study.

The level of striping of both individuals and groups has been shown to have no observable influence on group demographics, habitat choice and fecundity for the population of zebra in Addo Elephant National Park with the exception of females that had reproduced having fewer mean stripes in total and across the legs and head versus those that had not; although the observed difference here was small. Indeed, the finding that females who possess fewer stripes in these body regions reproduced more, while statistically significant, it is difficult to argue that this difference is of biological importance given the small difference in number of stripes. Establishing whether such a small difference in striping is something that has not been previously studied and it may be difficult to do. Studies concerning ectoparasitic resistance

and thermoregulation do tend to quantify levels of striping with observed effect sizes (Caro, 2014; Egri et a., 2013; Hovarth et al., 2018) but replicating this approach in work focused on a social aspect of striping would be far more difficult. The analysis performed here was, however, limited by a relatively small sample size and probable imperfect identification of resampling. It was deemed too subjective in this case to identity mother/foal pairs in the time frame allowed. Identification of such pairing has been conducted in previous work and an effort was made to emulate this, however these works operated with captive populations on a notably longer and more in-depth timescale than this work allowed; in the case of Pluhacek (et al., 2014) this constituted several years of observation (Olleova et al., 2014; Pluhacek et al., 2013).

It is not surprising that no effect of striping was observed on the composition of harems and that the striping of stallions in particular bore no relation to actual or potential reproductive success given that both sexes, stallions and bachelor males were shown to have similar degrees of striping across all body sections. This further suggest that sexual selection with stripes as a signal is unlikely to be occurring in plains zebra. This study is the first to test for differences in the number of stripes between demographic groups in plains zebra. A key limitation here is that only the number of stripes were considered in analysis. Further work concerning the morphology and condition of striping may prove interesting, however.

Due to limitations in the sampling period and study population the question as to whether the degree of striping plays a role in the fecundity of individuals cannot be said to be completely addressed. A longer study period would allow for higher quality data especially in evaluating individuals reproductive output. This study does, however, take the first step in suggesting that stripes play little to no role in the reproductive practices of plains zebra. Furthermore, in typical frameworks for sexual selection, ornamentation represents an honest cost to the

ornamented individual (Anderson, 1994; Anderson & Iwasa, 1996; Clutton-Brock, 2007). Given that striping is laid down during gestation in zebra (Johnathon, 1977) it is difficult to suggest that there is meaningful cost to stripes, with little to prevent individuals becoming more stripy if stripes are a desirable trait. Interestingly, differences in the number of stripes, both as a whole and across individual body sections, were established between both sexes and age categories for the Addo population. Such differences have not been established previously and there may be several plausible explanations regarding this variance.

### Fecundity and sexual selection:

Plains zebra are known as being a highly social species with high degree of stability in their social aggregations (Klingel, 1971; Rubenstein, 2010). The variability encountered in group composition was therefore somewhat surprising. No compelling evidence was found to support the idea that striping within the context of these aggregations may be related to greater fecundity. This may be down to the relatively short sampling period, imprecision in determining resampling and the way in which stable groups were defined within this work.

The question of sexual selection in species with unapparent or cryptic dimorphism is an area that has received relatively limited attention in the literature (West-Eberhard, 1983; Montgomerie & Lyon, 2012; Lyon & Montgomerie, 2012). To date most of the work conducted concerning this has been confined to avifauna, primates and invertebrates (Candolin, 2003; Hare & Simmons, 2019; Hunter & Bussiere, 2019; Rigaill et al., 2019). Females were shown to have more torso striping than males; although this difference was rather small and females that were deemed to have reproduced had fewer stripes on average than those who had not. If stripes were involved in sexual selection, one would expect the reverse to be true with males possessing greater striping given that plains zebra reproduce within a harem.

Given that work concerning female mate choice and ornamentation has begun to successfully establish that some species display a seemingly atypical sexual selection, it was deemed plausible that this may be the case for zebra. However, there are key differences in the type of dimorphism found in species where both sexes have been shown to be selective and possess exaggerated ornaments (Lyon & Montgomerie, 2012; Montgomerie & Lyon, 2012; West-Eberhard, 1983). In the case of mandrill both sexes have been documented as being choosy and there is a degree of competition for mates between them, however there is still a marked body size and ornamentation difference between the sexes with multiple levels of selection likely occurring as part of a complex social system (Setchell, 2016).

There is also a clear cost to the types of dimorphism found in cases like this where ornamentation acts as an honest signal of fitness or other desirable trait. There is no apparent cost to striping and thus there is little to limit stripe morphology as striping it is laid down in early foetal development (Johnathon, 1977). Yet, striping varies from species to species with each seemingly maintaining an optimal number of stripes across a population. Indeed, if sheer number of stripes was a desirable trait in sexual selection for zebra, one would expect runaway selection for striping, clearly this is not the case. It is possible however, that a cost lies in maintaining stripe quality although no predetermined mechanism exists for this. This aspect of striping was not incorporated in this work. This is problematic when considering most of the proposed mechanisms for the origin of zebra stripes.

The short sampling period provided little more than a snapshot of reproductive success of individuals across their lifespan. Given its prevalence across taxa, it would also be reasonable to assume a level of sneaky mating among this population of zebra. Without more in depth effort to follow specific individuals and groups there was no way to capture any possible effects this may be having (King & Gurnell, 2007). It is inconsistent with prevailing sexual

selection theory that a creature that produces within harems does not express a degree of sexual dimorphism (Emlen & Oring, 1988; Hargreaves & Eckert, 2014). In equids, it would be reasonable to assume that this dimorphism does occur within zebra but the mechanism by which this occurs is not fully understood.

Despite these issues, this work goes some way to stating that striping is not a significant factor influencing harem composition or wider reproductive success in plains zebra. Nor do stripes play a seemingly direct role in the number of juveniles produced either by a group or a particular stallion with the exception of females with fewer stripes reproducing more; although this result is limited by a paucity of a clear biological reason for this and issues with data collection and analysis as potentially important factors including paternity and reproductive success over a lifespan were not captured in this study. Striping may yet play a role in the mating behaviours of zebra, but this cannot be asserted based on the results of this work.

## Differences in striping between ages and sexes:

All the observed differences in striping between demographic groups, while statistically significant, were less than 10 stripes difference. It is difficult to argue that this difference is of biological importance, however this cannot be ruled out. Juveniles possessed significantly more leg striping than their adult counterparts, females possessed significantly more stripes on the torso than males and females who were taken to have reproduced possess fewer stripes than females that had not. Several mechanisms may be at play influencing these observed differences. The increased number of leg stripes in juveniles may represent a form of stabilising selection may be at play whereby a selection pressure is being exerted to normalise the adaptive trait that had been artificially altered in the zebra population during the Quagga Project. As seen in figure 1, the quagga was devoid of striping below the belly, on the legs and

backwards from the mid-point on the torso. Given that, as a relic from the project, the striping of the Addo population of zebra is likely to be deficient in these areas and there is a response in the population toward normalising striping to an optimal stable state. If this is the case, this is the first instance that a normalizing selection pressure has been observed in zebra. For this to be the case a selection pressure must be exerted on these portions of the body. Nevertheless, the underlying mechanism by which this selection is driven remains unknown. There are three possibilities driving this increase. 1. It is possible that zebra may be preferentially breeding with pairs with greater leg striping relative to the deficiency of stripes in these body regions throughout the adult population. However, this was not captured in the within harem analysis nor did stallions or reproducing females show significantly greater leg striping compared with other individuals. 2. Juveniles with more leg stripes are more likely to have survived until detection. Rates of loss for juveniles are relatively high and admittance into the group for mother foal pairs usually takes 1-2, this may weeks which may leave the juvenile particularly susceptible to threats from predation and biting fly attack (Klingel, 1969; Smuts 1976). 3. Alternatively, the observed higher rates of leg striping in juveniles may be a developmental phenomenon.

Juveniles of numerous species exhibit heightened levels of camouflaging markings with many experimental studies tending to focus on shore crabs (*Carcinus maenas*) due to their ease to work with (Gluckman & Cardoso, 2009; Kelman et al., 2006; Palma & Steneck, 2001; Stevens, 2016; Stuart-Fox et al., 2009). Surprisingly, very little work has been conducted attempting to discern why this is the case especially where colour change occurs over a long period. Generally, the most applied assumption is that such markings offer an adaptive benefit in the form of crypsis. If this is the case, however, then the usefulness of these markings must diminish with age as most species lose them over time (Clark, 1976). This is not surprising if

the behaviour and ecology of juveniles and adults is markedly different. Juveniles are likely less able to evade predation and must rely more heavily on crypsis. For this to be achieved the juvenile's appearance must, to a high degree, match their background (Stevens & Merliaita, 2009). Anecdotally, juvenile zebra were noticed to be striped to a higher degree in the field. There was a feeling, however that juveniles, as with other species, became less striped over time; in a similar fashion to the way lowland tapir juveniles and other juvenile mammals lose markings over time (Caro, 2013; Clark, 1976; Gilmore, 2007). This proved impossible to test as the means by which individuals were recognised and recoded relied on stripes being consistent over resamples. Zebra are unique in retaining a very high degree of striping into adulthood. If, in the case of zebra, crypsis is not the key mechanism driving striping, something that cannot be entirely discounted, then the mechanism that drives stripes might also be of particular importance to juveniles around the leg region. Caro (et al., 2014) noted that striping of the legs may be particularly useful in ectoparasitic resistance. They argued that leg striping tended to have an unusually high frequency and that biting flies tend to fly at a height matching that of the legs. Naturally, this height is markedly different for adult and juvenile zebra. Perhaps it is not the height that is most important in this case, rather an innate vulnerability of this region from parasites.

For this to be true, ectoparasitic attack must be a sufficiently powerful driver to enact a change in zebra survival and breeding success and juvenile survival over a relatively short period of time. The diseases spread by biting flies are certainly potent in equids and can be both the principal cause of fatality in individuals and reduce overall fitness increasing the likelihood of death by other means (Foil, 1989; Krinsky, 1976; Mulles, 2002). The range of bacterium, viruses and other parasites spread by tabanid flies is very large with one of only eleven solely equine diseases, the equine infectious anaemia virus (EIAV), being transmitted

through this vector (Baldacchino et al., 2013; Cook et al., 2013). EIAV is a retrovirus that causes can develop either chronically or acutely. In its acute form EIAV causes sudden fever and swelling within the animal which may lead to death. In its chronic form the virus causes bouts of fever and weight loss over a long period usually until death (Cook et al., 2013). Other than the direct spread of infection, biting flies remove a significant amount of blood from their hosts and cause a considerable amount of annoyance reducing the time spent foraging in wild species (Baldacchino et al., 2013b; Foil and Hogsette, 1994). Clearly attack from biting flies can pose a serious risk to zebra and the severity of their impact effect may be greater on juveniles. However, it remains unclear as to where flies could cause age related differences in striping or whether this is merely a developmental phenomenon.

It is certainly possible that striping in zebra is not set until sometime after birth. Turing (1952), devised a model by which regular patterns in animals, including zebra, are predictably laid down according to a difference in the quantity of morphogens in cell formation from a nearly stable state to an unstable state. This process may well continue after birth in plains zebra leading to temporal variation in stripe patterns as an individual ages (Gravan & Lahoz-Beltra, 2004; Marcon & Sharpe 2012).

Females possessed marginally more stripes in total and across the torso than males. This would suggest that striping might be of more importance to females, perhaps due to the extra cost of bearing offspring. The method by which the distinction between females that had and had not reproduced was, however, coarse and heavily limited by the short timeframe in which fieldwork was undertaken. It would be reasonable to assert that if striping is a benefit to individuals then it may be of more importance to females than males, as the cost of gestation makes the female role more costly overall. If there is a benefit of stripes, then that benefit would be felt most strongly by females. Certainly, the cost of reproduction can lead to more

time allocated to feeding in other equids (Boyd, 1988; Rubenstein, 1994). Yet females that reproduced were shown to have fewer stripes than those that did not. This may be another instance whereby a normalising selection pressure is being exerted if those females were reproducing with males of higher than mean striping. This was not, however, shown to be the case with the available evidence. With reproducing females having fewer stripes on average, their striping is brought down to similar levels of males on average. However, it is difficult to establish sound biological relevance for this finding. Stripes may play a role in selecting for the most similarly striped, in terms of quantity, individuals with which to reproduce. Alternatively, striping may be a signal for optimal breeding a marker of genetic compatibility as found in numerous species in the form of the major histocompatibility complex (Penn, 2002; Huchard et al., 2010). As an extension of this, it is conceivable that stripes may aid in kin recognition and inbreeding avoidance if stripes are representative of those genetics. Other, including the house mouse (Mus musculus), species do this with chemical signals (Winn et al., 1986). Equids are known to use olfactory signals in this way, which may make striping surplus to requirements as a signal of genetic quality (Antczak & Allen, 1989). Future work, especially focusing on stripe morphology as well as quantity, would be beneficial in understanding the importance of striping in this context.

### Stripe counting:

The geometry and relative position of striping may be a factor of importance when considering stripes in a social context; this has already been evidenced in studies concerning ectoparasitic resistance (Blaho et al., 2013; Caro, 2016; Egri et al., 2012). If zebra are capable of recognising each other using stripes it would be a reasonable assumption that these characteristics would be of importance, as well as stripe number. Other species with more traditional body size and

clear ornamentation dimorphism are known to value both the presence and quality of ornamentation in their socially reproductive practices (Chenoweth et al., 2006; Delope & Moller, 1997; Mays & Hill, 2004). Unfortunately, no satisfactory method pre-existed for quantifying these factors and no method was developed in this work to do so. However, an important step in establishing whether stripes can have an evolutionarily driven origin is determining whether striping is itself a heritable trait. The work of the Quagga Project and a recent works by Larison (2015) and Parsons (et al., 2007) found that this was indeed the case.

An initial effort was made to digitise the means by which stripes were counted from imagery. This transpired to be prohibitively difficult and open to error. Given this, the decision was made to count stripes by hand according to an altered existing method (Harley's stripe scoring system) (Quagga project, 2005). Due to this, an unknown degree of error is likely to have occurred during the stripe counting process. This system was developed as part of the Quagga Project, which attempted to back breed plains zebra to resemble quagga (Quagga project, 2005). The benefit of study the Addo population of plans zebra was that they likely possess an artificially high range in striping, due selective breeding as part of the Quagga Project. While useful for the purposes of this study it could also be argued that the striping of this population is somewhat unnatural and therefore conclusions drawn from them must be interpreted in a semi-natural fashion.

### Stripe recognition:

Underpinning all of the work conducted concerning zebra striping and their social ecology is the assumption that zebra are capable of perceiving and recognising each other's stripes. We know that domestic horses can recognise each other both visually and audibly (Proops et al., 2009) but no such work has been extended to zebra. This is understandable given the difficulties in finding a test population however, it is not inconceivable. The difficulty in

addressing this question might lie in isolating stripes as a marker for recognition; over other visual, audible and olfactory stimuli. The assumption that zebra can recognise one another's striping is one that has been made in this work also. Addressing this question would be highly beneficial for work going forward given that other equids have can use several methods to identify one another. To assume that stripes play any role in identification of conspecifics without evidence is potentially something of leap, striping may serve another purpose entirely.

### **Conclusion:**

The observed differences in striping between age categories, with juveniles being more striped across the legs, may lend weight to the ectoparasitic theory given that young zebra are likely more at risk from parasitic attack. This difference offers the interesting suggestion that a normalising selection pressure is being exerted on the Addo Elephant National Park population of plains zebra. It would be exceedingly interesting to establish whether a degree of striping is lost as a juvenile matures in a similar fashion found on lowland tapir. This would help address the questions raised by the heightened striping found on juveniles. Clearly, without holistically understanding a trait both in terms of benefit and cost, is imperative in understating its evolution. If striping were a marker for optimal breeding as with MHC in other species the cost of striping becomes of less importance as the trait is not generally desirable throughout the population, rather it is specific to certain individuals. While this is potentially plausible, other species have developed olfactory signals for achieving this and there is no reason to suggest that this is not the case for zebra also (Huchard et al., 2010; Penn, 2002).

The question of cost becomes particularly problematic when assigning a sexual selection value to stripes. One would expect the decline of a trait that bore no cost to an ornamented male in

a classical sexual selection model. But given that in the case of zebra both sexes possess stripes, conventional sexual selection could not be at play. Indeed, no link was established between the degree of striping of stallions and groups and their respective reproductive outputs. This is not surprising given that fitting even an atypical sexual selection model to this species runs into difficulties. The finding that females with fewer stripes reproduced more must also be viewed with caution due the small observed difference in stripes and the lack of clear biological significance of this.

While there may be no obvious cost to stripes, there is evidence to suggest that there is a differing level of cost in inter-birth intervals by sex of the foal. The inter-birth period after a male foal has been born is longer than that of a female one, thus the costs of reproducing each sex differ (Barnier et al., 2012). Given that no difference in striping was observed between sexes and that it is difficult to attribute a cost to stripe in themselves it would be incorrect to suggest that stripes play a role in the wider reproductive processes in plains zebra. Regardless, without a cost of striping it is difficult to apply even an atypical model. The results presented here suffer from a paucity of data in both quantity and quality, however. A key step forward in future work concerning zebra striping and possible links to reproductive behaviours and wider social system would be considering stripe morphology as well as quantity. The conjecture surrounding this topic has tended to argue for a single driver for stripiness. It may prove beneficial in future work to consider the cumulative beneficial effects stripes may have.

The challenging task of determining the evolutionary mechanism by which an adaptive trait is derived is necessarily complex. When considering something, such as striping in zebra, from a mechanistic viewpoint the temptation is to seek answers in a linear fashion. An attempt has been made here to avoid this pitfall and consider numerous factors relating to the ecology of plains zebra, which may have an additive impact when driving something so pronounced as

striping in this species. The most supported theory, that of ectoparasitic resistance, suggest that striping is highly effective at deterring landing rates of biting flies and that certain geometries are better than others at achieving this (Blaho et al., 2013; Caro, 2016; Caro et al., 2014; Egri et a., 2012; Lyons & Goldstien, 2018). These studies do not detail if there is an upper maximum to this effect, although eventually one must be met. If there is little cost to developing stripes, then one would expect striping to match a pattern and frequency optimal to deterring parasites if this theory is to be taken as solely true. Furthermore, striping as found on all zebra species is very extreme when compared to other striped mammals. Given the myriad potential benefits of striping it is notably conspicuous that this extreme in stripes is limited to only these species. However, it seems very likely that stripes do help deter ectoparasitic attack, but it is certainly plausible that this is only one of their functions. Further work refining the current literature will help lend further clarity to the topic.

# References:

- Allen, W. L., I. C. Cuthill, N. E. Scott-Samuel and R. Baddeley. (2011), 'Why the Leopard Got Its Spots: Relating Pattern Development to Ecology in Felids', *Proceedings of the Royal* Society B-Biological Sciences Vol. 278, No. 1710, pp. 1373-1380.
- Álvarez-García, G., Frey, C. F., Mora, L. M. O., & Schares, G. (2013). A century of bovine besnoitiosis: an unknown disease re-emerging in Europe. *Trends in Parasitology*, 29(8), 407-415.
- Andersson, M. B. (1994). Sexual selection. Princeton University Press.
- Andersson, M. and Y. Iwasa. (1996), 'Sexual Selection', *Trends in Ecology & Evolution* Vol. 11, No. 2, pp. 53-58.
- Antczak, D. F., & Allen, W. R. (1989). Maternal immunological recognition of pregnancy in equids. *Journal of reproduction and fertility. Supplement*, *37*, 69-78.
- Baldacchino, F., Gardes, L., De Stordeur, E., Jay-Robert, P., & Garros, C. (2014). Blood-feeding patterns of horse flies in the French Pyrenees. *Veterinary parasitology*, *199*(3-4), 283-288.
- Baldacchino, F., Muenworn, V., Desquesnes, M., Desoli, F., Charoenviriyaphap, T., & Duvallet, G. (2013). Transmission of pathogens by Stomoxys flies (Diptera, Muscidae): a review. *Parasite*, 20.
- Barnett, J. B., A. S. Redfern, R. Bhattacharyya-Dickson, O. Clifton, T. Courty, T. Ho, A. Hopes, T. McPhee, K. Merrison, R. Owen, N. E. Scott-Samuel and I. C. Cuthill. (2017), 'Stripes for Warning and Stripes for Hiding: Spatial Frequency and Detection Distance', *Behavioral Ecology* Vol. 28, No. 2, pp. 373-381.
- Barnier, F., S. Grange, A. Ganswindt, H. Ncube and P. Duncan. (2012), 'Inter-Birth Interval in Zebras Is Longer Following the Birth of Male Foals Than after Female Foals', Acta Oecologica-International Journal of Ecology Vol. 42, pp. 11-15.
- Bartlam-Brooks, H. L. A., K. Roskilly, C. Buse, J. C. Lowe, E. Bennitt, T. Y. Hubel and A. M. Wilson. (2017), 'Determining Water Intake in Wild Plain's Zebra (Equus Quagga)', *Integrative and Comparative Biology* Vol. 57, pp. E9-E9.
- Basile, M., S. Boivin, A. Boutin, C. Blois-Heulin, M. Hausberger and A. Lemasson. (2009),
   'Socially Dependent Auditory Laterality in Domestic Horses (Equus Caballus)', Animal Cognition Vol. 12, No. 4, pp. 611-619.
- Bauer, I. E., J. McMorrow and D. W. Yalden. (1994), 'The Historic Ranges of 3 Equid Species in Northeast Africa - a Quantitative Comparison of Environmental Tolerances', *Journal of Biogeography* Vol. 21, No. 2, pp. 169-182.

- Blaho M, Egri A, Szaz D, Kriska G, Akesson S, Horvath G (2013) Stripes disrupt odour attractiveness to biting horseflies: battle between ammonia, CO<sub>2</sub>, and colour pattern for dominance in the sensory systems of host-seeking tabanids. Physiol Behav 119 168–74.
- Boyd, L. E. (1988). Time budgets of adult Przewalski horses: effects of sex, reproductive status and enclosure. *Applied Animal Behaviour Science*, *21*(1-2), 19-39.
- Brady, J. and W. Shereni. (1988), 'Landing Responses of the Tsetse-Fly Glossina-Morsitans-Morsitans Westwood and the Stable Fly Stomoxys-Calcitrans (L) (Diptera, Glossinidae and Muscidae) to Black-and-White Patterns - a Laboratory Study', *Bulletin of Entomological Research* Vol. 78, No. 2, pp. 301-311.
- Brady J, Shereni W (1988) Landing responses of the tsetse fly Gossina morsitans morsitans
   Westwood and the stable fly *Stomoxys calcitrans* (L.) (Diptera: Gossinidae & Muscidae) to black-and-white patterns: a laboratory study. Bull Ent Res 78: 301–311.
- Britten, K. H., T. D. Thatcher and T. Caro. (2016), 'Zebras and Biting Flies: Quantitative Analysis of Reflected Light from Zebra Coats in Their Natural Habitat', *Plos One* Vol. 11, No. 5, pp. 15.
- Burnham, K.P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach.* Berlin, Germany: Springer.
- Candolin, U. (2003), 'The Use of Multiple Cues in Mate Choice', *Biological Reviews* Vol. 78, No. 4, pp. 575-595.
- Caro, T., A. Izzo, R. C. Reiner, H. Walker and T. Stankowich. (2014), 'The Function of Zebra Stripes', *Nature Communications* Vol. 5, pp. 10.
- Caro, T. I. M. (2013, June). The colours of extant mammals. In *Seminars in cell & developmental biology* (Vol. 24, No. 6-7, pp. 542-552). Academic Press.
- Caro, T. (2017). "Zebra Stripes". University of Chicago Press (7 Feb. 2017)
- Chenoweth, S. F., P. Doughty and H. Kokko. (2006), 'Can Non-Directional Male Mating Preferences Facilitate Honest Female Ornamentation?', *Ecology Letters* Vol. 9, No. 2, pp. 179-184.
- Chihota, C. M., Rennie, L. F., Kitching, R. P., & Mellor, P. S. (2001). Mechanical transmission of lumpy skin disease virus by Aedes aegypti (Diptera: Culicidae). *Epidemiology & Infection*, 126(2), 317-321.
- Clark, W. C. (1976). The environment and the genotype in polymorphism. *Zoological Journal of the Linnean Society*, *58*(3), 255-262.
- Cloudsley-Thompson, J. L. (1984), 'How the Zebra Got His Stripes New Solutions to an Old Problem', *Biologist* Vol. 31, No. 4, pp. 226-228.

- Clutton-Brock, T. (2007), 'Sexual Selection in Males and Females', *Science* Vol. 318, No. 5858, pp. 1882-1885.
- Clutton-Brock, T. (2009), 'Sexual Selection in Females', *Animal Behaviour* Vol. 77, No. 1, pp. 3-11.
- Cook, R. F., Leroux, C., & Issel, C. J. (2013). Equine infectious anemia and equine infectious anemia virus in 2013: a review. *Veterinary microbiology*, *167*(1-2), 181-204.

Couzin, I. D., & Krause, J. (2003). Self-organization and collective behavior in vertebrates.

Darwin, C. R. In 'The Descent of Man, and Selection in Relation to Sex'. Vol. 2. (John Murray, 1871).

- Delope, F. and A. P. Moller. (1993), 'Female Reproductive Effort Depends on the Degree of Ornamentation of Their Mates', *Evolution* Vol. 47, No. 4, pp. 1152-1160.
- DeMenocal, P. B. (2004), 'African Climate Change and Faunal Evolution During the Pliocene-Pleistocene', *Earth and Planetary Science Letters* Vol. 220, No. 1-2, pp. 3-24.
- Desquesnes, M., Holzmuller, P., Lai, D. H., Dargantes, A., Lun, Z. R., & Jittaplapong, S. (2013). Trypanosoma evansi and surra: a review and perspectives on origin, history, distribution, taxonomy, morphology, hosts, and pathogenic effects. *BioMed research international*, 2013.
- Egri, A., M. Blaho, G. Kriska, R. Farkas, M. Gyurkovszky, S. Akesson and G. Horvath. (2012), 'Polarotactic Tabanids Find Striped Patterns with Brightness and/or Polarization Modulation Least Attractive: An Advantage of Zebra Stripes', *Journal of Experimental Biology* Vol. 215, No. 5, pp. 736-745.
- Emlen, S. T. and L. W. Oring. (1988), 'Citation Classic Ecology, Sexual Selection, and the Evolution of Mating Systems', *Current Contents/Agriculture Biology & Environmental Sciences*, No. 8, pp. 12-12.
- Fischhoff, I. R., J. Dushoff, S. R. Sundaresan, J. E. Cordingley and D. I. Rubenstein. (2009), 'Reproductive Status Influences Group Size and Persistence of Bonds in Male Plains
- Zebra (Equus Burchelli)', Behavioral Ecology and Sociobiology Vol. 63, No. 7, pp. 1035-1043.
- Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, H. M. Larkin, M. J. Sellier and D. I. Rubenstein. (2007), 'Social Relationships and Reproductive State Influence Leadership Roles in Movements of Plains Zebra, Equus Burchellii', *Animal Behaviour* Vol. 73, pp. 825-831.
- Foil, L. D. (1989), 'Tabanids as Vectors of Disease Agents', *Parasitology Today* Vol. 5, No. 3, pp. 88-96.
- Foil, L. D., & Hogsette, J. A. (1994). Biology and control of tabanids, stable flies and horn flies. *Revue scientifique et technique-Office international des épizooties*, 13(4), 1125-1158.

- Fugazzola, M. C. and L. Stancampiano. (2012), 'Host Social Rank and Parasites: Plains Zebra (Equus Quagga) and Intestinal Helminths in Uganda', *Veterinary Parasitology* Vol. 188, No. 1-2, pp. 115-119.
- Funston, P. J., M. G. L. Mills and H. C. Biggs. (2001), 'Factors Affecting the Hunting Success of Male and Female Lions in the Kruger National Park', *Journal of Zoology* Vol. 253, pp. 419-431.
- Georgiadis, N. (1985), 'Growth-Patterns, Sexual Dimorphism and Reproduction in African Ruminants', *African Journal of Ecology* Vol. 23, No. 2, pp. 75-87.
- Gilmore, M. (2007). Tapir behavior: An examination of activity patterns, mother-young interactions, spatial use, and environmental effects in captivity on two species (Tapirus indicus and Tapirus bairdii). Oklahoma State University.
- Ginsberg, J.R. (1989) The ecology of female behaviour and male mating success in the Grevy's Zebra. Symnp. Zool. Soc. Lond. 61, 89-110
- Gluckman, T. L. and G. C. Cardoso. (2010), 'The Dual Function of Barred Plumage in Birds: Camouflage and Communication', *Journal of Evolutionary Biology* Vol. 23, No. 11, pp. 2501-2506.
- Godfrey, D., J. N. Lythgoe and D. A. Rumball. (1987), 'Zebra Stripes and Tiger Stripes the Spatial-Frequency Distribution of the Pattern Compared to That of the Background Is Significant in Display and Crypsis', *Biological Journal of the Linnean Society* Vol. 32, No. 4, pp. 427-433.
- Gough, K. F. and G. I. H. Kerley. (2006), 'Demography and Population Dynamics in the Elephants Loxodonta Africana of Addo Elephant National Park, South Africa: Is There Evidence of Density Dependent Regulation?', *Oryx* Vol. 40, No. 4, pp. 434-441.
- Grafen, A. (1984). Natural selection, kin selection and group selection. *Behavioural ecology: An* evolutionary approach, 2, 62-84.
- Grange, S., F. Barnier, P. Duncan, J. M. Gaillard, M. Valeix, H. Ncube, S. Periquet and H. Fritz. (2015), 'Demography of Plains Zebras (Equus Quagga) under Heavy Predation', *Population Ecology* Vol. 57, No. 1, pp. 201-214.
- Gravan, C. P., & Lahoz-Beltra, R. (2004). Evolving morphogenetic fields in the zebra skin pattern based on Turing's morphogen hypothesis. *International Journal of Applied Mathematics and Computer Science*, *14*, 351-361.
- Groves, C. P. (1986), 'The Taxonomy, Distribution and Adaptations of Recent Equids', *Beihefte zum Tuebinger Atlas des Vorderen Orients Reihe A Naturwissenschaften*, pp. 11-65.
- Groves, C. P. and C. H. Bell. (2004), 'New Investigations on the Taxonomy of the Zebras Genus Equus, Subgenus Hippotigris', *Mammalian Biology* Vol. 69, No. 3, pp. 182-196.

- Gutierrez, C., Desquesnes, M., Touratier, L., & Büscher, P. (2010). Trypanosoma evansi: recent outbreaks in Europe. *Veterinary parasitology*, *174*(1-2), 26-29.
- Hack, M. A., R. East and D. I. Rubenstein. (2002), 'Status and Action Plan for the Plains Zebra (Equus Burchellii)', In P. D. Moehlman (Ed.), *Equids: Zebras, Asses and Horses: Status Survey and Conservation Action Plan.*, lucn.
- Hall, M. J. R., R. Farkas and J. E. Chainey. (1998), 'Use of Odour-Baited Sticky Boards to Trap Tabanid Flies and Investigate Repellents', *Medical and Veterinary Entomology* Vol. 12, No. 3, pp. 241-245.
- Hanggi, E. B. and J. F. Ingersoll. (2009), 'Long-Term Memory for Categories and Concepts in Horses (Equus Caballus)', *Animal Cognition* Vol. 12, No. 3, pp. 451-462.
- Hansen, T. F. (1997), 'Stabilizing Selection and the Comparative Analysis of Adaptation', *Evolution* Vol. 51, No. 5, pp. 1341-1351.
- Hare, R. M. and L. W. Simmons. (2019), 'Sexual Selection and Its Evolutionary Consequences in Female Animals', *Biological Reviews* Vol. 94, No. 3, pp. 929-956.
- Hargreaves, A. L. and C. G. Eckert. (2014), 'Evolution of Dispersal and Mating Systems Along Geographic Gradients: Implications for Shifting Ranges', *Functional Ecology* Vol. 28, No. 1, pp. 5-21.
- Harley, E. H., M. H. Knight, C. Lardner, B. Wooding and M. Gregor. (2009), 'The Quagga Project: Progress over 20 Years of Selective Breeding', South African Journal of Wildlife Research Vol. 39, No. 2, pp. 155-163.
- Hayward, M. W. (2006), 'Prey Preferences of the Spotted Hyaena (Crocuta Crocuta) and Degree of Dietary Overlap with the Lion (Panthera Leo)', *Journal of Zoology* Vol. 270, No. 4, pp. 606-614.
- Hayward, M. W. and G. I. H. Kerley. (2005), 'Prey Preferences of the Lion (Panthera Leo)', Journal of Zoology Vol. 267, pp. 309-322.
- Hildreth, E. C. and C. Koch. (1987), 'The Analysis of Visual-Motion from Computational Theory to Neuronal Mechanisms', *Annual Review of Neuroscience* Vol. 10, pp. 477-533.
- Hoekstra, H. E., J. M. Hoekstra, D. Berrigan, S. N. Vignieri, A. Hoang, C. E. Hill, P. Beerli and J. G. Kingsolver. (2001), 'Strength and Tempo of Directional Selection in the Wild', *Proceedings of the National Academy of Sciences of the United States of America* Vol. 98, No. 16, pp. 9157-9160.
- Horvath, G., J. Majer, L. Horvath, I. Szivak and G. Kriska. (2008), 'Ventral Polarization Vision in Tabanids: Horseflies and Deerflies (Diptera : Tabanidae) Are Attracted to Horizontally Polarized Light', *Naturwissenschaften* Vol. 95, No. 11, pp. 1093-1100.

- Horvath, G., A. Pereszlenyi, D. Szaz, A. Barta, I. M. Janosi, B. Gerics and S. Akesson. (2018), 'Experimental Evidence That Stripes Do Not Cool Zebras', *Scientific reports* Vol. 8, No. 1, pp. 9351.
- Horvath, G., Pereszlényi, Á., Åkesson, S., & Kriska, G. (2019). Striped bodypainting protects against horseflies. *Royal Society open science*, 6(1), 181325.
- How, M. J. and J. M. Zanker. (2014), 'Motion Camouflage Induced by Zebra Stripes', *Zoology* Vol. 117, No. 3, pp. 163-170.
- Howie, J., & Pomiankowski, A. (2016). Female sneak copulation. *Encyclopedia of evolutionary* psychological science, 1-5.
- Huchard, E., Raymond, M., Benavides, J., Marshall, H., Knapp, L. A., & Cowlishaw, G. (2010). A female signal reflects MHC genotype in a social primate. *BMC evolutionary biology*, 10(1), 96.
- Hunt, J., C. J. Breuker, J. A. Sadowski and A. J. Moore. (2009), 'Male-Male Competition, Female Mate Choice and Their Interaction: Determining Total Sexual Selection', *Journal of Evolutionary Biology* Vol. 22, No. 1, pp. 13-26.
- Hunter, F. D. L. and L. F. Bussiere. (2019), 'Comparative Evidence Supports a Role for Reproductive Allocation in the Evolution of Female Ornament Diversity', *Ecological Entomology* Vol. 44, No. 3, pp. 324-332.
- Ireland, H. M. and G. D. Ruxton. (2017), 'Zebra Stripes: An Interspecies Signal to Facilitate Mixed-Species Herding?', *Biological Journal of the Linnean Society* Vol. 121, No. 4, pp. 947-952.
- Iyengar, V. K. and B. D. Starks. (2008), 'Sexual Selection in Harems: Male Competition Plays a Larger Role Than Female Choice in an Amphipod', *Behavioral Ecology* Vol. 19, No. 3, pp. 642-649.
- Jacquiet, P., Liénard, E., & Franc, M. (2010). Bovine besnoitiosis: epidemiological and clinical aspects. *Veterinary parasitology*, *174*(1-2), 30-36.
- Jarman, P. (1983), 'Mating system and sexual dimorphism in large terrestrial, mammalian herbivores'. Biological Reviews, 58: 485-520. doi:10.1111/j.1469-185X.1983.tb00398.x
- Jennions, M. D. and M. Petrie. (1997), 'Variation in Mate Choice and Mating Preferences: A Review of Causes and Consequences', *Biological Reviews* Vol. 72, No. 2, pp. 283-327.
- Jonathan, B. L. (1977), A unity underlying the different zebra striping patterns. Journal of Zoology, 183: 527-539. doi:10.1111/j.1469-7998.1977.tb04204.x
- Johnstone, R. A., J. D. Reynolds and J. C. Deutsch. (1996), 'Mutual Mate Choice and Sex Differences in Choosiness', *Evolution* Vol. 50, No. 4, pp. 1382-1391.

- Jones, A.G., Ratterman, N.L. (2009). 'Mate choice and sexual selection: What have we learned since Darwin?' *The Proceedings of the National Academy of Sciences of the United States of America* Vol. 106, pp 10001-10008.
- Junker, K., Horak, I. G., & Penzhorn, B. (2015). History and development of research on wildlife parasites in southern Africa, with emphasis on terrestrial mammals, especially ungulates. *International Journal for Parasitology: Parasites and Wildlife*, 4(1), 50-70.
- Karpestam, E., S. Merilaita and A. Forsman. (2014), 'Natural Levels of Colour Polymorphism Reduce Performance of Visual Predators Searching for Camouflaged Prey', *Biological Journal of the Linnean Society* Vol. 112, No. 3, pp. 546-555.
- Karpestam, E., Merilaita, S., & Forsman, A. (2018), 'Size Variability Effects on Visual Detection Are Influenced by Colour Pattern and Perceived Size', *Animal Behaviour* Vol. 143, pp. 131-138.
- Kelman, E. J., P. Tiptus and D. Osorio. (2006), 'Juvenile Plaice (Pleuronectes Platessa) Produce Camouflage by Flexibly Combining Two Separate Patterns', *Journal of Experimental Biology* Vol. 209, No. 17, pp. 3288-3292.
- Kingdon, J. (1984). The zebra's stripes: an aid to group cohesion. In: Macdonald D, editor. The encyclopedia of mammals, London: Allen & Unwin, London. p. 486–7.
- King, S. R. B. and J. Gurnell. (2007), 'Scent-Marking Behaviour by Stallions: An Assessment of Function in a Reintroduced Population of Przewalski Horses (Equus Ferus Przewalskii)', *Journal of Zoology* Vol. 272, No. 1, pp. 30-36.
- Kjernsmo, K. and S. Merilaita. (2012), 'Background Choice as an Anti-Predator Strategy: The Roles of Background Matching and Visual Complexity in the Habitat Choice of the Least Killifish', *Proceedings of the Royal Society B-Biological Sciences* Vol. 279, No. 1745, pp. 4192-4198.
- Klingel, H. (1969). The social organisation and population ecology of the plains zebra (Equus quagga). African Zoology, 4(2).
- Klingel, H. (1971). 'A Comparison of the Social Behaviour of the Equidae' *The University of Calgary Press* Vol 1, pp 124 -132.
- Knight, C. L. (2017), 'How the Zebra Got Its Stripes: Darwinian Stories Told through Evolutionary Biology', *Library Journal* Vol. 142, No. 7, pp. 103-103.
- Kokko H, Johnstone RA: Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling.
   Philosophical Transactions of the Royal Society of London Series B. 2002, 357: 319-330. 10.1098/rstb.2001.0926.
- Kokko H, Monaghan P: Predicting the direction of sexual selection. Ecology Letters. 2001, 4: 159-165. 10.1046/j.1461-0248.2001.00212.x.

- Krause, J., Ruxton, G. D., Ruxton, G. D., & Ruxton, I. G. (2002). *Living in groups*. Oxford University Press.
- Krinsky, W. L. (1976), 'Animal-Disease Agents Transmitted by Horse Flies and Deer Flies (Diptera-Tabanidae)', *Journal of Medical Entomology* Vol. 13, No. 3, pp. 225-275.
- Larison, B., R. J. Harrigan, H. A. Thomassen, D. I. Rubenstein, A. M. Chan-Golston, E. Li and T. B. Smith. (2015), 'How the Zebra Got Its Stripes: A Problem with Too Many Solutions', *Royal Society Open Science* Vol. 2, No. 1, pp. 10.
- Lahiri, M., Tantipathananandh, C., Warungu, R., Rubenstein, D. I., & Berger-Wolf, T. Y. (2011, April). Biometric animal databases from field photographs: identification of individual zebra in the wild. In *Proceedings of the 1st ACM international conference on multimedia retrieval* (p. 6). ACM.
- Lea, J. M. D., G. I. H. Kerley, H. Hrabar, T. J. Barry and S. Shultz. (2016), 'Recognition and Management of Ecological Refugees: A Case Study of the Cape Mountain Zebra', *Biological Conservation* Vol. 203, pp. 207-215.
- Lehmann, L. and N. Perrin. (2003), 'Inbreeding Avoidance through Kin Recognition: Choosy Females Boost Male Dispersal', *American Naturalist* Vol. 162, No. 5, pp. 638-652.
- Leuthold, W., (1977). 'African Ungulates: A Comparative Review of Their Ethology and Behavioural Ecology', Springer-Verlag Berlin Heidelberg. Vol 8.
- Lorenzen, E. D., P. Arctander and H. R. Siegismund. (2008), 'High Variation and Very Low Differentiation in Wide Ranging Plains Zebra (Equus Quagga) Insights from Mtdna and Microsatellites', *Molecular Ecology* Vol. 17, No. 12, pp. 2812-2824.
- Lovrovich, P., C. Sighieri and P. Baragli. (2015), 'Following Human-Given Cues or Not? Horses (Equus Caballus) Get Smarter and Change Strategy in a Delayed Three Choice Task', *Applied Animal Behaviour Science* Vol. 166, pp. 80-88.
- Lyon B.E., Montgomerie R. (2012) Sexual selection is a form of social selection. Phil. Trans. R. Soc. B 367, 2266–2273
- Lyons, B. and D. Goldstein. (2018), 'Visible Spectrum Polarization Characterization of Equus Zebra Hartmannae Hide' 20th Conference on Polarization - Measurement, Analysis, and Remote Sensing XIII, Spie-Int Soc Optical Engineering.
- Marcon, L., & Sharpe, J. (2012). Turing patterns in development: what about the horse part? *Current opinion in genetics & development*, 22(6), 578-584.
- Maresca, C., Scoccia, E., Faccenda, L., Zema, J., & Costarelli, S. (2012). Equine infectious anemia: active surveillance in central Italy 2007-2009. Journal of Equine Veterinary Science, 32(9), 596-598.

- Marshall, F. and C. Asa. (2013), 'A Study of African Wild Ass Behavior Provides Insights into Conservation Issues, Domestication Processes and Archaeological Interpretation', *Journal of Archaeological Method and Theory* Vol. 20, No. 3, pp. 479-494.
- Martin, R. A. and D. W. Pfennig. (2009), 'Disruptive Selection in Natural Populations: The Roles of Ecological Specialization and Resource Competition', *American Naturalist* Vol. 174, No. 2, pp. 268-281.
- Mays, H. L. and G. E. Hill. (2004), 'Choosing Mates: Good Genes Versus Genes That Are a Good Fit', *Trends in Ecology & Evolution* Vol. 19, No. 10, pp. 554-559.
- Mills, M. G. L. and H. C. Biggs. (1993), 'Prey Apportionment and Related Ecological Relationships between Large Carnivores in Kruger-National-Park', *Mammals as Predators*, No. 65, pp. 253-268.
- Moehlman, P. D., F. Kebede and H. Yohannes. (1998), 'The African Wild Ass (Equus Africanus): Conservation Status in the Horn of Africa', *Applied Animal Behaviour Science* Vol. 60, No. 2-3, pp. 115-124.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tamlbing, C.J., Hayward, M.W., (2016). 'Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores', Ecology, 97(5), 2016, pp. 1123–1134.
- Moloo, S. K., Kabata, J. M., & Gitire, N. M. (2000). Study on the mechanical transmission by tsetse fly Glossina morsitans centralis of Trypanosoma vivax, T. congolense or T. brucei brucei to goats. *Acta tropica*, 74(1), 105-108.
- Montgomerie, R., Lyon B.E., (2012) The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Phil. Trans. R. Soc. B 367, 2274–2293.
- Morris, D (1990) Animal watching. 'A field guide to animal behavior'. Johnathan Cape, London.
- Mousseau, T. A. and D. A. Roff. (1987), 'Natural-Selection and the Heritability of Fitness Components', *Heredity* Vol. 59, pp. 181-197.
- Mullens, B. A. (2019). Horse flies and deer flies (Tabanidae). In *Medical and veterinary entomology* (pp. 327-343). Academic Press.
- Neuhaus, P. and K. E. Ruckstuhl. (2002), 'The Link between Sexual Dimorphism, Activity Budgets, and Group Cohesion: The Case of the Plains Zebra (Equus Burchelli)', *Canadian Journal of Zoology-Revue Canadienne De Zoologie* Vol. 80, No. 8, pp. 1437-1441.
- Olleova, M., J. Pluhacek and S. R. B. King. (2012), 'Effect of Social System on Allosuckling and Adoption in Zebras', *Journal of Zoology* Vol. 288, No. 2, pp. 127-134.

- Owaga, M. L. (1975), 'The Feeding Ecology of Wildebeest and Zebra in Athi Kaputei Plains', East African Wildlife Journal Vol. 13, No. 3/4, pp. 375-383.
- Palma, A. T. and R. S. Steneck. (2001), 'Does Variable Coloration in Juvenile Marine Crabs Reduce Risk of Visual Predation?', *Ecology* Vol. 82, No. 10, pp. 2961-2967.
- Parsons, R., C. Aldous-Mycock and M. R. Perrin. (2007), 'A Genetic Index for Stripe-Pattern Reduction in the Zebra: The Quagga Project', *South African Journal of Wildlife Research* Vol. 37, No. 2, pp. 105-116.
- Pedersen, C. E. T., A. Albrechtsen, P. D. Etter, E. A. Johnson, L. Orlando, L. Chikhi, H. R. Siegismund and R. Heller. (2018), 'A Southern African Origin and Cryptic Structure in the Highly Mobile Plains Zebra', *Nature Ecology & Evolution* Vol. 2, No. 3, pp. 491-498.
- Penn, D. J. (2002), 'The Scent of Genetic Compatibility: Sexual Selection and the Major Histocompatibility Complex', *Ethology* Vol. 108, No. 1, pp. 1-21.
- Penzhorn, B. L. (1984), 'A Long-Term Study of Social-Organization and Behavior of Cape Mountain Zebras Equus-Zebra-Zebra', *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology* Vol. 64, No. 2, pp. 97-146.
- Periquet, S., P. Richardson, E. Z. Cameron, A. Ganswindt, L. Belton, E. Loubser and F. Dalerum. (2017), 'Effects of Lions on Behaviour and Endocrine Stress in Plains Zebras', *Ethology* Vol. 123, No. 9, pp. 667-674.
- Pluhacek, J., L. Bartos and L. Culik. (2006), 'High-Ranking Mares of Captive Plains Zebra Equus Burchelli Have Greater Reproductive Success Than Low-Ranking Mares', *Applied Animal Behaviour Science* Vol. 99, No. 3-4, pp. 315-329.
- Pluhacek, J., M. Olleova, L. Bartos and J. Bartosova. (2014), 'Time Spent Suckling Is Affected by Different Social Organization in Three Zebra Species', *Journal of Zoology* Vol. 292, No. 1, pp. 10-17.
- Pluhacek, J., M. Olleova, J. Bartosova, J. Pluhackova and L. Bartos. (2013), 'Laterality of Suckling Behaviour in Three Zebra Species', *Laterality* Vol. 18, No. 3, pp. 349-364.
- Proops, L. and K. McComb. (2012), 'Cross-Modal Individual Recognition in Domestic Horses (Equus Caballus) Extends to Familiar Humans', *Proceedings of the Royal Society B-Biological Sciences* Vol. 279, No. 1741, pp. 3131-3138.
- Proops, L., K. McComb and D. Reby. (2009), 'Cross-Modal Individual Recognition in Domestic Horses (Equus Caballus)', Proceedings of the National Academy of Sciences of the United States of America Vol. 106, No. 3, pp. 947-951.
- Quagga Project. Management Plan for the "Quagga Project", South Africa National Parks. 2005
- Reusch, T. B. H., M. A. Haberli, P. B. Aeschlimann and M. Milinski. (2001), 'Female Sticklebacks Count Alleles in a Strategy of Sexual Selection Explaining Mhc Polymorphism', *Nature* Vol. 414, No. 6861, pp. 300-302.
- Roberts, S. C. and L. M. Gosling. (2003), 'Genetic Similarity and Quality Interact in Mate Choice Decisions by Female Mice', *Nature Genetics* Vol. 35, No. 1, pp. 103-106.
- Rubenstein, D. I. (1994). The ecology of female social behavior in horses, zebras, and asses. *Animal societies: individuals, interactions, and organization*, 13-28.
- Rubenstein, D. I. (2010), 'Ecology, Social Behavior, and Conservation in Zebras', In R. Macedo (Ed.), Advances in the Study of Behavior: Behavioral Ecology of Tropical Animals.
- Rueffler, C., T. J. M. Van Dooren, O. Leimar and P. A. Abrams. (2006), 'Disruptive Selection and Then What?', *Trends in Ecology & Evolution* Vol. 21, No. 5, pp. 238-245.
- Ruxton, G. D. (2002), 'The Possible Fitness Benefits of Striped Coat Coloration for Zebra', Mammal Review Vol. 32, No. 4, pp. 237-244.
- Sankey, C., S. Henry, N. Andre, M. A. Richard-Yris and M. Hausberger. (2011), 'Do Horses Have a Concept of Person?', *Plos One* Vol. 6, No. 3, pp. 4.
- Schaller, G. B. (1972), 'The Serengeti Lion a Study of Predator Prey Relations', *The Serengeti Lion a Study of Predator Prey Relations*, pp. 480.
- Schulze, R. E., Lynch, S. D., & Maharaj, M. (2007). Annual precipitation. South African Atlas of Climatology and Agrohydrology: Water Research Commission, Pretoria, RSA, WRC Report 1489/1/06, Section 6.2.
- Scott-Samuel, N. E., R. Baddeley, C. E. Palmer and I. C. Cuthill. (2011), 'Dazzle Camouflage Affects Speed Perception', *Plos One* Vol. 6, No. 6, pp. 5.
- Setchell, J. M. (2016). Sexual Selection and the differences between the sexes in M andrills (M andrillus sphinx). *American journal of physical anthropology*, *159*, 105-129.
- Shon, D., G. Piao, Y. Kim and J. Lee. (2017), 'Cfd Modelling of Air Temperature Reduction and Airflow Induced by the Use of Chilled Wall Panels Based on the Biological Principles of Zebra Stripes', Architectural Science Review Vol. 60, No. 6, pp. 507-515.
- Simpson, H. I., S. A. Rands and C. J. Nicol. (2012), 'Social Structure, Vigilance and Behaviour of Plains Zebra (Equus Burchellii): A 5-Year Case Study of Individuals Living on a Managed Wildlife Reserve', *Acta Theriologica* Vol. 57, No. 2, pp. 111-120.
- Sjöström, M., Ardö, J., Arneth, A., Boulain, N., Cappelaere, B., Eklundh, L., de Grandcourt, A., Kutsch, W., Merbold, L. and Nouvellon, Y. (2011). Exploring the potential of MODIS EVI for modeling grossprimary production across African ecosystems. Remote Sensing of Environment, 115(4), pp.1081-1089.

- Smakhtina, O. (1998), 'Historical Changes in Rainfall Pattern in the Eastern Cape Province, South Africa', Water Resources Variability in Africa During the Xxth Century, No. 252, pp. 135-142.
- Smuts, G.L. (1976). 'Reproduction in the zebra stallion (*Equus burchelli antiquorum*) from the Kruger National Park' from the Kruger National Park, Zoologica Africana, 11:1, 207-220
- Stevens, M. (2016), 'Color Change, Phenotypic Plasticity, and Camouflage', *Frontiers in Ecology and Evolution* Vol. 4, pp. 10.
- Stevens, M. and S. Merilaita. (2009), 'Animal Camouflage: Current Issues and New Perspectives', *Philosophical Transactions of the Royal Society B-Biological Sciences* Vol. 364, No. 1516, pp. 423-427.
- Stevens, M., W. T. L. Searle, J. E. Seymour, K. L. A. Marshall and G. D. Ruxton. (2011), 'Motion Dazzle and Camouflage as Distinct Anti-Predator Defenses', *Bmc Biology* Vol. 9, pp. 11.
- Stevens, M., D. H. Yule and G. D. Ruxton. (2008), 'Dazzle Coloration and Prey Movement', Proceedings of the Royal Society B-Biological Sciences Vol. 275, No. 1651, pp. 2639-2643.
- Stoner, C. J., T. M. Caro and C. M. Graham. (2003), 'Ecological and Behavioral Correlates of Coloration in Artiodactyls: Systematic Analyses of Conventional Hypotheses', *Behavioral Ecology* Vol. 14, No. 6, pp. 823-840.
- Stuart-Fox, D. and A. Moussalli. (2009), 'Camouflage, Communication and Thermoregulation: Lessons from Colour Changing Organisms', *Philosophical Transactions of the Royal* Society B-Biological Sciences Vol. 364, No. 1516, pp. 463-470.
- Thayer GH (1909) Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: Being a summary of Abbott H. Thayer's discoveries. Macmillan, London.
- Tobias, J. A., R. Montgomerie and B. E. Lyon. (2012), 'The Evolution of Female Ornaments and Weaponry: Social Selection, Sexual Selection and Ecological Competition', *Philosophical Transactions of the Royal Society B-Biological Sciences* Vol. 367, No. 1600, pp. 2274-2293.
- Tong, W. F., B. Shapiro and D. I. Rubenstein. (2015), 'Genetic Relatedness in Two-Tiered Plains Zebra Societies Suggests That Females Choose to Associate with Kin', *Behaviour* Vol. 152, No. 15, pp. 2059-2078.
- Turell, M. J., & Knudson, G. B. (1987). Mechanical transmission of Bacillus anthracis by stable flies (Stomoxys calcitrans) and mosquitoes (Aedes aegypti and Aedes taeniorhynchus). *Infection and immunity*, 55(8), 1859-1861.
- Turing, A. M. (1990). The chemical basis of morphogenesis. *Bulletin of mathematical biology*, 52(1-2), 153-197.

- Vlok, J. H. J., D. I. W. Euston-Brown and R. M. Cowling. (2003), 'Acocks' Valley Bushveld 50 Years On: New Perspectives on the Delimitation, Characterisation and Origin of Subtropical Thicket Vegetation', *South African Journal of Botany* Vol. 69, No. 1, pp. 27-51.
- Waage, J. K. (1981), 'How the Zebra Got Its Stripes Biting Flies as Selective Agents in the Evolution of Zebra Coloration', *Journal of the Entomological Society of Southern Africa* Vol. 44, No. 2, pp. 351-358.
- Wallace, A. R. Mimicry, and other protective resemblances among animals. *Westminster Foreign Q Rev.* 31, 1–43 (1867).
- Wedekind, C., T. Seebeck, F. Bettens and A. J. Paepke. (1995), 'Mhc-Dependent Mate Preferences in Humans', *Proceedings of the Royal Society B-Biological Sciences* Vol. 260, No. 1359, pp. 245-249.
- Weel, S., L. H. Watson, J. Weel, J. A. Venter and B. Reeves. (2015), 'Cape Mountain Zebra in the Baviaanskloof Nature Reserve, South Africa: Resource Use Reveals Limitations to Zebra Performance in a Dystrophic Mountainous Ecosystem', *African Journal of Ecology* Vol. 53, No. 4, pp. 428-438.
- West-Eberhard M.J., (1983) Sexual selection, social competition and speciation. Q. Rev. Biol. 55, 155–183
- Winn, B. E., & Vestal, B. M. (1986). Kin recognition and choice of males by wild female house mice (Mus musculus). *Journal of Comparative Psychology*, 100(1), 72.

## **Acknowledgements:**

My thanks to Dr. Matt Hayward and Dr. Graeme Shannon for their expert supervision. My thanks also to Will Connock and Dan Smith who were admirable co-workers during fieldwork and beyond. My gratitude to the James Pantyfedwyn Foundation and Coalbourn Trust for help funding this project; also, to Dr. Graham Kerley and SAN Parks for their aid and cooperation throughout. Lastly, thanks must be given to both my family and Maresa Bradley for their much-needed moral support.