

Wildlife Conservation Research Unit (WildCRU)

Department of Zoology,
University of Oxford

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The Conservation Biology of the African Golden Cat

Ms Laila Bahaa-el-din

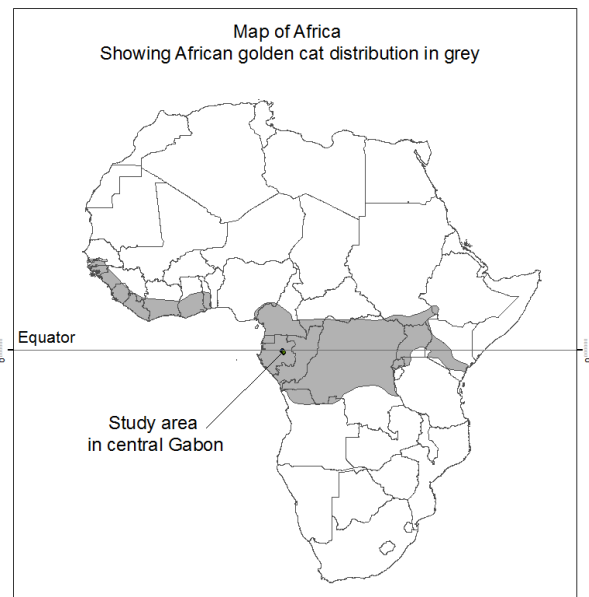
Introduction and background

The African golden cat (*Caracal aurata* or *Profelis aurata*) project in Gabon began in 2010 when the need for baseline information on this almost unstudied felid was recognised. The organisation, Panthera, initiated the project and continues to support it through a Kaplan Graduate Award to Laila Bahaa-el-din, in partnership with WildCRU and the University of KwaZulu-Natal.

Although Africa is recognised for its big cats, the golden cat is the only cat on the continent to depend on forest habitat. Its range is restricted to equatorial Africa (see map, right). Threats such as bushmeat hunting, forest clearing for agriculture and commercial logging have caused an estimated 44% loss of golden cat habitat to date, but so little is known about this species that it is as yet impossible to state the extent to which human activities are really affecting it.

The African golden cat was previously believed to be the relative of the Asiatic golden cat but recent molecular evidence places it with the more open-habitat species, the caracal (*Caracal caracal*) and the serval (*Caracal serval* or *Leptailurus serval*). The genus name change to caracal for the golden cat and the serval has not yet been completely accepted and their previous names are therefore still widely used.

The golden cat is highly variable, with coat colour ranging from smoky-grey to reddish-brown. The level of spotting also varies, sometimes covering the cat's whole coat, and sometimes restricted to the underbelly and inner side of limbs. Coat colours are not restricted to geographic area as all varieties have been recorded across their range, with skins of black (melanistic) individuals also in collections. There does appear to be a geographical gradient in the extent of spotting, with cats in the west often more densely spotted than those to the east.



Left: Grey morph, and right: red morph of the African golden cat (© Laila Bahaa-el-din/Panthera)

The field studies that have been carried out to date have focused on forest carnivore diets, and the golden cat's diet was found to consist mostly of rodents and small ungulates (blue duikers in particular). A study on leopards in the rainforest found that leopards sometimes prey on golden cats and there is also dietary overlap between the two species, with competition likely to occur.



Left: Leopard compete with and prey on the African golden cat (© Laila Bahaa-el-din/Panthera)

Goals and achievement towards them

- 1) **To establish a protocol for monitoring golden cats using remote camera traps**
We carried out a pilot study in 2010 to test a method widely used for many other felid species – remotely-triggered camera traps – to collect data on golden cats. This study took place over four months at the Mikongo Conservation Centre in Lopé National Park in central Gabon. During this time, we photo-captured golden cats on 37 occasions, which indicated that this tool can be used with satisfactory results for golden cat data collection. The study also highlighted some technical considerations that needed to be taken into account if we wanted to be able to use these data to make density estimates, one of our key goals. For example, golden cat individuals can be identified through their unique coat patterns, but we found that cameras with infra-red flashes, though more discreet, did not take clear enough photographs for identification. The camera trap spacing we used was also found to be too wide for golden cats. This information was useful when designing our on-going work.
- 2) **To obtain baseline data on African golden cats in a healthy ecosystem**
Between August–November 2011, we used camera traps to survey golden cats in the Langoué region of Ivindo National Park. This area has no recent history of logging or hunting and is therefore pristine, primary forest. The only activities to have taken place in this area in recent times are small-scale tourism and research. We had 37 independent captures of golden cats at 22 out of our 38 trapping sites over the course of approximately 6 weeks. We are in the process of identifying individuals in order to make density estimates for this site, which will enable us to ascertain whether golden cats are naturally rare as is often stated, or if they can live at quite high densities when undisturbed.

3) To assess how commercial logging affects golden cat populations

Between May–August 2011, we undertook camera trap surveys in the Milolé region of the CEB logging concession (managed by the company Precious Woods Gabon). The area had been logged 2 years prior to commencement of the survey and active logging was taking place nearby. Precious Woods are recognised as having high standards of management in terms of sustainable exploitation and keeping their impacts on biodiversity to a minimum. The latter is achieved by the company blocking and monitoring road access and strictly enforcing hunting regulations with their staff. We had 47 individual captures of golden cats at 19 out of our 40 trapping sites in about 6 weeks of trapping. Again, we will now identify the individuals and make density estimates for this area.

Comparing results from our pristine site and this sustainably logged forest will give us some insight into how logging affects golden cat populations. From a superficial look at the data, the number of captures seems quite high, and it may indicate that golden cats can do quite well in logged forest, but we will need to wait on density results to see if this high number of captures translates into high numbers of individuals.

However, the Precious Woods logging concession is not representative of the majority of concessions in central Africa and so another logged site in central Gabon will be surveyed in 2012. A logging concession that is more representative will be selected where management has dedicated less attention to the impact of their exploitation on biodiversity. A comparison between our environmentally-responsible logging concession and this less-responsible one will indicate whether measures put in place by Precious Woods are effective in maintaining golden cat populations.



Left: Logging taking place in Gabon. Right: Logging roads are opened to extract the wood. It is these roads that let hunters/poachers in to otherwise inaccessible areas. (© Tim Rayden)

4) To assess how bushmeat hunting affects golden cat populations

A site where bushmeat hunting occurs will be surveyed in 2012 and results will be compared to those from the pristine site. Not only will we see how golden cat densities are affected by hunting, but we will also look into the potential reasons for this. Often, the most important factor in determining the presence and density of a predator is the

abundance of its prey, and our camera trap data will enable us to compare prey abundance across our study sites.



Left: A village hunter sets a wire snare. Golden cats are frequently caught in snares. Right: Blue duikers killed for bushmeat. This small ungulate is a common prey species of the golden cat. (© Lauren Coad).

- 5) **To gain insight into the competitive relationship between golden cats and leopards**
Golden cat and leopard scats are being collected at all study sites to establish what prey species they are eating, and the level of overlap between the two species' diets. Results will be compared across sites to see whether competition increases at disturbed sites where prey abundance may be reduced. Camera trap data from all sites will also be used to see whether golden cats use spatial and/or temporal segregation to avoid leopards.
- 6) **To understand how golden cats and other carnivores are perceived by local communities with regard to conflict, cultural beliefs, and as a source of bushmeat**
This will be examined through the use of interviews with local communities that will begin in 2012. Golden cats on one hand are believed to be hyper-sensitive to human presence, and on the other are accused of coming into villages and killing chickens, sheep and goats. Golden cats may be being mis-identified as the perpetrators, or they may be less reclusive than thought. Interviews will be conducted with the use of images to reduce the risk of mis-identification.

Other questions will include whether or not there are any traditional uses for golden cat parts, and whether they are consumed as bushmeat. Anecdotal evidence indicates that golden cat tails are used as good-luck charms in some parts of their range and that they are frequently caught in wire snares and are eaten.
- 7) **To raise awareness about this almost unknown cat**
The African golden cat is a species that very few people have heard of, and so is rarely taken into account in conservation strategies and policy-making, such as putting in place hunting regulations. Through the collection of useful information on the golden cat and with the use of images and video, we hoped to raise the profile of this cat and show its potential as a flagship species for the equatorial forests of Africa.

A big achievement in 2011 was the video capture of a golden cat that sat down in front of a camera trap [image 8]. This footage received wide viewership when it was picked up by the media, including CNN, Reuters, National Geographic, and more (see <http://www.panthera.org/african-golden-cats-0>). Importantly, this footage also received coverage in newspapers, magazines and on websites in Gabon where local people have been made more aware of how rare and special this cat is.



A frozen image of the video footage that gained wide media attention in 2011
(© Laila Bahaa-el-din/Panthera)

- 8) **To prepare and implement a conservation strategy for the golden cat**
This will take place on completion of data collection and analysis, and will include identifying important areas for golden cat conservation, and advising governments and private institutions, such as logging companies, on measures they can take to ensure a future for golden cats.

Investigating cheetah ecology and coexistence with other large carnivores in Northern Botswana

Ms Femke Broekhuis

With <10'000 individuals left in the wild, the cheetah (*Acinonyx jubatus*) is scrambling for survival. This is due to threats, such as habitat fragmentation and human-wildlife conflict. Less studied, however, are the possible effects that other carnivore species might have on cheetah success and survival. Previous research has suggested that lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) have a negative influence on cheetah populations (Marker, Dickman et al. 2003) both through the stealing of kills and direct predation.



Figure 1: A spotted hyaena attempting to steal a kill from one of the collared cheetah
(© Femke Broekhuis)

As a result there have been several studies that have illustrated that cheetah directly avoid lions and spotted hyaenas (Durant 2000; Durant 2000; Hunter, Durant et al. 2007) but quantitative evidence of the influence of lion and spotted hyaena on cheetah behaviour is still scarce.

With the use of GPS technology and field observations, Femke Broekhuis has been investigating the fine-scale mechanisms that enable cheetah to coexist with sympatric large African carnivores, and to gain a better understanding of the complexity of the ecological and behavioural relationships between cheetah, lion and spotted hyaena.

The main objectives of this project are to determine:

- if the activity patterns of cheetah are influenced by the presence and activity patterns of lion and spotted hyaena.
- the extent to which spatial distribution patterns of cheetah are influenced by the spatial distribution patterns of lion and spotted hyaena.

This research, which began in October 2008, is carried out in the pristine Okavango Delta ecosystem in Northern Botswana. In order to collect the necessary data, several cheetah, lion and spotted hyena were fitted with GPS radio-collars which automatically collect data on where the animals have been (location) and their activity.



Figure 2: Researcher, Femke Broekhuis, fitting a collar on a female cheetah (© Gabriele Cozzi)

Despite Botswana being one of the largest remaining strongholds for cheetah and supporting a healthy population of lion and spotted hyena, these species have received very little attention in this area. It was therefore important to estimate the current densities of these three carnivore species. Lion and spotted hyena densities were established through direct observations and through the use of calling stations (Ogutu and Dublin 1998). As cheetah are rare, elusive and range over large areas (average home-range 789 km²), cheetah density estimates were based on both incidental sightings and photographs taken by camera traps (Figure 3). The current density estimate for cheetah in this area is approximately 0.6 individuals/100km². This estimate lies between 0.25 individuals/100km² found in Namibia and 0.8–1.0 individuals/100km² found in Serengeti National Park, Tanzania.



Figure 3: Camera traps are used to estimate cheetah densities in the Okavango Delta in Northern Botswana – left, a photograph of one of the males with a GPS radio-collar, and right a photograph of a known, uncollared male (© Femke Broekhuis).

Using the activity data from the GPS collars, the daily activities of each of the three species were investigated to determine the degree of temporal segregation. The previously observed diurnal activity of cheetah has been assumed to result from the need to avoid encounters with the stronger, nocturnal lion and spotted hyaena. However, the activity data from the collars revealed an unexpectedly high degree nocturnal activity of cheetah. The nocturnal activity of cheetah made up 50% of their diel activity budget and their activity was in sync with the phases of the moon, becoming more active as the moonlight increased and less active when the moonlight decreased (Figure 4). The lunar cycle did not affect the activity of lion and spotted hyaena (data not shown).

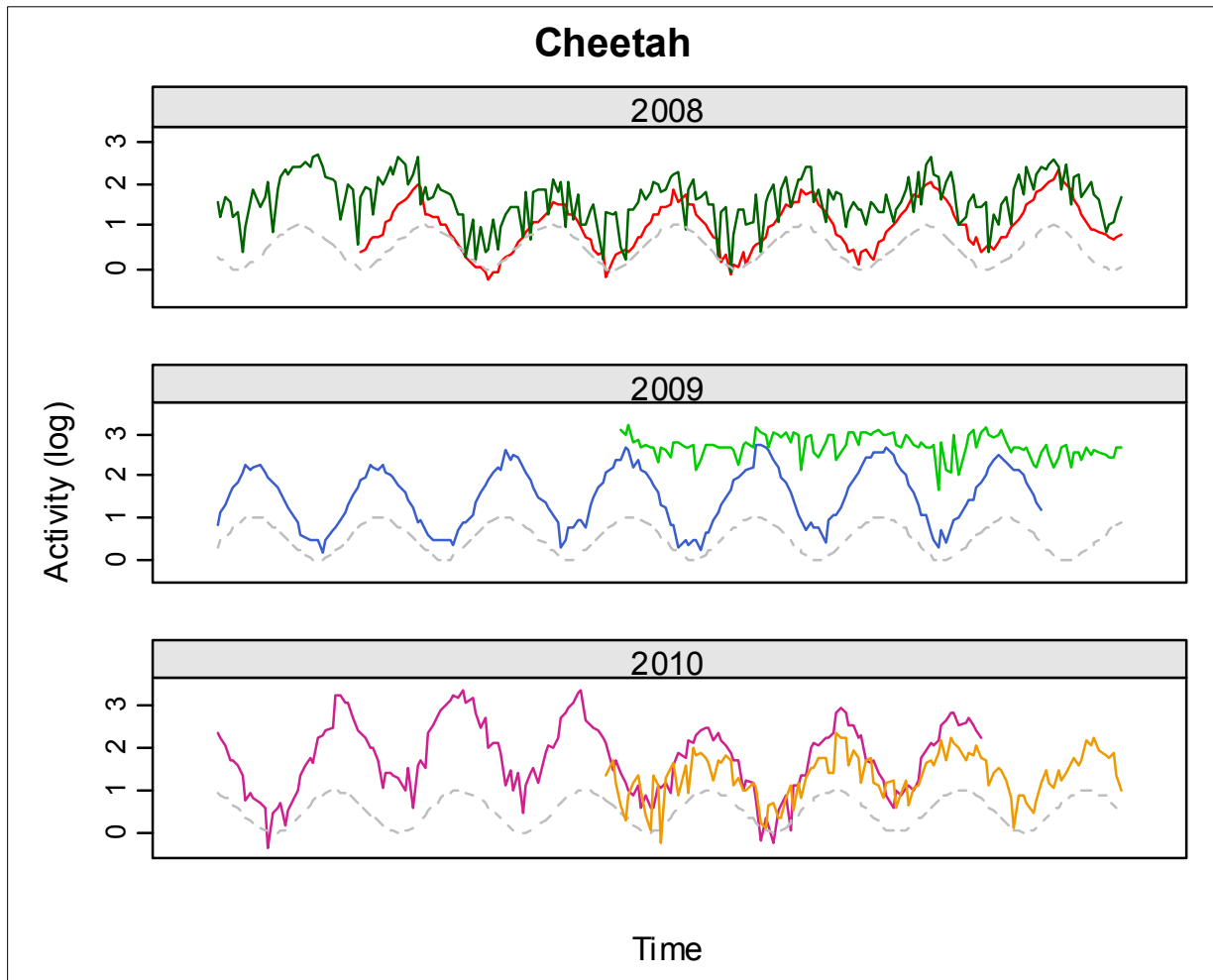


Figure 4: Fitted values from mixed-effects models showing the nocturnal activity patterns of cheetah ($n = 6$) during the dry season in three consecutive years. Each colour represents a different individual. Variation in moonlight intensity is depicted for comparison in each panel (grey dotted line; not to scale). One male cheetah (#3, light green) shows consistently high nocturnal activity.

These results indicate that the nocturnal activity of cheetah are primarily constrained by moonlight availability, rather than by the nocturnal activity of the dominant lion and hyena. The fact that cheetah do not seem to avoid lion and hyaena in time suggests that spatial avoidance and the availability of 'refuges' might be more important than was previously thought. The next step of the analysis will be to look at the habitat use and spatial distribution of cheetah in relation to the probability of encountering either lion or spotted hyaena. By understanding the mechanisms by which cheetah coexist with other large carnivores, management policies can be developed to enhance cheetah survival in areas where all three carnivore species occur sympatrically, moving conservation towards a multi-species, rather than the conventional single-species, approach.

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Reintroductions

Dr Lauren Harrington

Reintroductions of either captive-bred or translocated animals have become an increasingly important part of conservation, and WildCRU has been involved in a number of such projects, both in the UK and overseas. Notably, Dr Tom Moorhouse carried out a series of experimental reintroductions that not only contributed to the restoration of the water vole in lowland England, but also demonstrated clearly the importance of habitat by showing that survival and population densities were higher at sites with higher vegetation abundance.



Left: water vole release, and right: water vole reintroduction site. (©Amy Isherwood)

In collaboration with Dr Tiit Maran at Tallinn zoo in Estonia, we introduced highly endangered, captive-bred European mink to the island sanctuary of Hiiumaa (from where the invasive American mink, the major threat to European mink, had previously been removed). And, following over a decade of deliberations, feasibility studies and public consultations (which our group contributed to with a number of scientific reviews and modelling exercises), we are now proud to carry out the role of Independent Monitoring Partners, with Scottish Natural Heritage (SNH), in the monitoring the ecology of the beavers that are the focus of the current 5-year trial release in the Knapdale Forest Estate in Scotland.



Beaver and Aspen (© Roo Campbell)

More generally, we recently carried out a systematic review of the (post-1990) scientific, and internet-based, literature on reintroductions of captive-bred, and wild-caught, animals (mammals, birds, amphibians and reptiles) to quantify the occurrence, and type, of welfare issues that may arise in these types of projects. A frequently referred to, but outmoded (and not very useful), dichotomy is that of 'populations' versus 'individuals', and, with that view in mind, the aims and strategies of conservation reintroductions and animal welfare have sometimes, in the past, been seen to clash.

Conservation reintroductions have a very clear aim: to restore a self-sustaining population of animals to their historical range – but it is not uncommon for individual animals to suffer in the process. Of course, populations are made up of individuals and greater consideration of animal welfare, therefore, has considerable potential for increasing conservation success insofar as those individuals in better 'condition' are more likely to survive, settle, and reproduce (and thus contribute to the establishment of the population). Yet, despite a growth in interest and concern for animal welfare, in farming, laboratory research, transport of animals, and zoos, welfare science has not yet entered mainstream conservation, and animal welfare is not always considered explicitly within conservation practice.

We reviewed 199 reintroduction projects, to find, perhaps not surprisingly, that over 80% of reports referred to success, and almost 40% referred to cost, but welfare, and more broadly 'ethics', were rarely mentioned. That is not to say that practitioners and researchers have not considered welfare (most universities, for example, have their own internal ethical review committees for all research that is carried out with animals), but the lack of information that is readily available means that future improvement is difficult, and potentially slow.

Potential welfare issues include, for example, high mortality rates (in the case that animals suffer because they are ill-prepared for life in the wild, or are placed in an environment that offers little chance of survival), dispersal or loss of animals (which may lead to animals suffering, or unable to feed, in inappropriate habitats) or human conflict (where this should have been resolved before animals were released). Most projects monitored aspects of reintroductions that might be, to some extent, indicative of animal welfare status – >70% projects monitored survival and 18% assessed body condition, but only 2% monitored stress levels (which would be more directly informative of the stress suffered by animals during release and the factors that increase, or decrease, it).

An example of our own work on animal welfare in this context is Dr Merryl Gelling's research on the impact of housing conditions during captivity on stress levels in water voles. That some level of stress will be involved is inevitable, but Merryl found that stress in water voles may be reduced by simply decreasing group size within the captive colony, or during transportation. Most (79%) of the projects we reviewed, carried out some type of supportive action that might improve welfare – most commonly use of on-site pre-release pens and provision of supplemental food or water – although, the extent and duration of support was variable and there appeared to be little empirical evidence as to what approach was most effective (or most beneficial for the animals).

Dr Lauren Harrington presented the findings of this review at the International Congress of Conservation Biology in New Zealand, in December 2011, and we hope, through publication of this work, to raise the profile of animal welfare amongst conservation biologists, and improve consideration of welfare in conservation practice.

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Bornean Clouded Leopard Programme:
Ecology and Conservation of a Tropical Forest Felid Guild

Mr Andrew J. Hearn and Ms Joanna Ross



Background

Recently declared a new species, having been found to be both genetically and morphologically distinct from the clouded leopard, *Neofelis nebulosa*, found on mainland Southeast Asia, the Diard's or Sunda clouded leopard, *Neofelis diardi*, is arguably the least known of the world's larger felids, with a distribution restricted to the islands of Sumatra and Borneo. The Sunda clouded leopard is the largest member of a unique guild of five felids found in Borneo's forests, other members include the Bornean bay cat, *Pardofelis badia*, marbled cat, *Pardofelis marmorata*, flat-headed cat, *Prionailurus planiceps*, and leopard cat, *Prionailurus bengalensis*. Two of these felids are classified by the IUCN as Endangered, two Vulnerable, and their presumed primary habitat is rapidly being lost, fragmented and/or altered in the region. The conservation status and ecology of none is well-known and the impact of anthropogenic habitat modification on each is obscure.

A new Bornean felid initiative

Initiated in June 2010, the Bornean Clouded Leopard Programme aims to advance the conservation of the Sunda clouded leopard and other threatened Bornean felids through a multi-disciplinary and multi-site conservation programme. The fundamental aim of this programme is to address the question: What is the distribution and conservation status of Sunda clouded leopards and other felids throughout Sabah, and what factors affect their presence and abundance? The answers will underpin research to tackle a subsequent question: What dispersal opportunities exist for clouded leopards and other Bornean felids in Sabah, and how might dispersal corridors be protected, enhanced and restored?



Sunda clouded leopard, captured at over 1,400m, in the Crocker Range. Previous studies suggested that these felids do not use forest above 1,300m in Borneo. (© Andrew Hearn/ WildCRU)

Working closely with the Sabah Wildlife Department (SWD), this three-year programme is being undertaken as a doctoral study by Andrew Hearn, with additional elements overseen by Joanna Ross, both based at WildCRU. The programme is primarily constructed around relatively short-term camera trap surveys designed to estimate clouded leopard densities and felid community structure in six key forest areas within Sabah. Presence data and density estimates of Sunda clouded leopard, their prey, and other felids across Sabah, including those in collaboration with other Bornean-felid researchers, will be used to prioritise areas in terms of importance for felids and will thus form the basis for a corridor analysis across Sabah and Borneo.

The principal aims of the programme are to:

- Establish the distributions and densities of Sunda clouded leopard and other Bornean wild cats within Sabah, and thereby to provide a baseline for subsequent monitoring.
- Assess the impacts of habitat alteration on, and habitat requirements of, Bornean wild cats, with a focus on the Sunda clouded leopard.
- Investigate Bornean felid ecology, including community structure, niche partitioning and intra-guild relationships.
- Ultimately, conduct a Borneo-wide corridor and landscape analysis, identifying existing clouded leopard corridors and suggesting large-scale actions in the context of forest loss.

Preliminary findings

This new Bornean felid initiative has been developed from three years of fruitful pilot studies, which were first launched in 2006, making it the longest running field study of Sunda clouded leopard and Bornean felids. We have now completed intensive camera trap surveys of seven key forest sites and two oil palm plantations in Sabah. Data continue to be analysed, and conclusions drawn, but several key findings are emerging:

Methodology

- We developed and refined a clouded leopard specific camera-trapping protocol suitable for the densely vegetated forest in Sabah, which can be adapted to similar forest regions throughout Borneo (Ross et al 2010)

Bornean felid responses to anthropogenic disturbance

- All five members of the Bornean felid guild can be found in selectively logged forest, further highlighting the conservation importance of this habitat (Ross et al, 2010)
- Oil palm plantations appear to be a non-habitat for all Bornean felids, apart from the more abundant, and adaptable, leopard cat (Ross et al, 2010).
- Of 6 presumed key clouded leopard prey species, all but the bearded pig avoid using oil palm, and thus the absence of clouded leopard from these habitats may be a result of reduced prey availability (Ross et al in prep, a)
- Our camera surveys provide tentative evidence that rehabilitated forest may support higher densities of clouded leopard than recently selectively logged forest (Hearn et al. Submitted), and we show that these declines may be linked to a decline in key prey species (Ross et al in prep, a).



Sunrise across a selectively logged Dipterocarp forest in Sabah. Our findings suggest that these modified landscapes are important habitats for the conservation of the Bornean felids.

(© Andrew Hearn)

Bornean felid ecology

- We radio-tagged the first, and to date only, Sunda clouded leopard, and in combination with the extensive camera data, conducted the first study on this felid's spatial ecology and activity (Hearn et al in prep).
- Our surveys have resulted in over 130,000 wildlife photographs, including 648 photos of Sunda clouded leopard, 133 marbled cat, 29 bay cat (including the first ever video), 4 flat-headed cat and 2,654 leopard cat, making it the largest Bornean felid photographic data set.



The Bornean bay cat. Incredibly, this species was first photographed only as recently as 2003, and even today there are only a handful of images of this beautiful felid, and it remains to be one of the real mysteries of the cat family. (© Joanna Ross & Andrew Hearn)

- These data are helping to shed light on Bornean felid guild ecology, and predator prey interactions (Ross et al in prep, b).

Next steps

We will shortly complete our camera survey of the Crocker Range National Park, which will provide the first clouded leopard density estimate from highland forest, and we will then move on to a further three forest sites, beginning with a resurvey of the Danum Valley. Our ongoing programme continues to build on our initial findings, and it is hoped that through the application of cutting edge conservation science, will contribute to the conservation of this unique guild of wild cats.



Deploying camera traps over more than 160km² often requires field teams to camp in the forest.
(© Andrew Hearn)

Reports and publications

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In addition to fieldwork, our project assists anti-poaching patrols in protected areas. Here members of our field team are recording the position of an illegal hunters camp within a National Park.

(© Kevin Hodge.)

The Badger Project: Life-history evolution and the role of senescence in badger ecology

Dr Chris Newman and Dr Christina Buesching

"Senescence has no function – it is the subversion of function."

Alex Comfort (Gerontologist / Social commentator 1920–2000)

In this report, we consolidate on some of our work through 2010–12 and we highlight the intricate interactions and trade-offs that occur during a badger's lifetime; crucial traits often overlooked when developing badger conservation measures.

Our central finding that different age classes face different stresses and exhibit different vulnerabilities has particular bearing on the on-going debate surrounding the management and implication of badgers in the transmission of bTB (Riordan et al. 2011). We hypothesise that a major contributor to the counter-productive perturbation effect observed to result from badger culling is the resultant failure of the residual population to respond adequately to exacerbated social stress. With individuals of different age classes varying in their capacities to mount adaptive responses to stress, it seems that age classes should not be treated with equivalent emphasis when developing bTB control policy.

A perplexing question in biology is how could evolution ever favour senescence; whereby the physiology of an individual declines through an aging process, along with a reduction in reproductive capacity – vulnerabilities that ultimately conclude in physical failure? Indeed, how could natural selection perpetuate the genes that cause aging, an apparent contradiction of Darwinian evolutionary theory?

As humans, we are very aware of the consequences of aging, and our place in societies responds to this reality. Almost all of the athletes performing at the London 2012 Olympics will be under 35. Almost all of the politicians planning these games will be more senior. And by age 65+ we hope to enjoy a more leisurely life-style free of the burdens of work, while hoping not to be relying too much on medication to keep us fit and active.

But what about mammals in the wild? They can't retire. They have no 'social security'. Indeed outside of a few eusocial species they have a very limited capacity, once mature, to change strategy through their lives. No matter how weary they may become, how crippled with geriatric disease, they must continue to seek out food, in the face of competition and possible predation – else they starve and die.

Having got to grips with many pieces of this puzzle from our 25 years of research at the Wytham Woods Badger Project – such as population dynamics, genetics, disease epidemiology, immunology and mating behaviour – we are now able to consider what shapes badger life-history dynamics and, in particular, how they cope with and respond to the aging process, as individuals, as members of a society and as species.

First of all, how could aging have evolved?

All organisms will eventually succumb to extrinsic mortality factors, such as trauma (accidents, predation), parasites and disease, etc., but why should there be a performance decline throughout life (aging)?

It used to be thought that since ancestral bacteria age, all other organisms must age. This is, however counter-intuitive; rather natural selection should favour the evolution of superior mechanisms for cellular maintenance, and hence avoid aging. Research is increasingly observing that species of fish, amphibians, and reptiles, do not show clear signs of senescence. Our perceptions of aging thus demonstrate a gerontological bias; it is we humans that age and the mammals on which we tend to rely.

Mammals evolved from reptilian ancestors, a taxon including many apparently non-aging species. All mammals exhibit physical decline and increasing intrinsic mortality with age. We are incapable of oocyst regeneration (resulting in menopause), have only two sets of teeth and can achieve only limited tissue regeneration. By contrast, reptiles regenerate teeth continuously and can regenerate entire limbs, they exhibit no reproductive senescence and do not decline with age. A pet iguana will not die from 'wearing out' as we would; rather it will die from a distinct proximal cause, such as infection, where the likelihood of mortality is a function of longevity.

Aging influences the schedule of investment mammals make in reproduction and survival – defining their life-history trade-offs. Organisms in hazardous environments will maximize reproduction (termed *r*-selected), exhibiting rapid development, small body sizes, and a short lifespan. Organisms in non-hazardous environments will maximize their performance up to environmental carrying capacity (termed *K*-selected) exhibiting delayed development, larger body sizes, and a longer lifespan.

It seems that aging evolved as a unique event in mammals, during the age of dinosaurs. Fundamentally, the force of natural selection declines with longevity, due to individuals succumbing to extrinsic mortality factors: the stronger the influence of these factors, the shorter the average lifespan. Proto-mammals, coexisting with dinosaurs, were smaller than modern rats and at the bottom of the food chain. Our mammalian ancestors did not have the opportunity to 'grow old' rather they were *r*-selected and desperate to leave offspring before they themselves were eaten. By this same token, their abilities to avoid being eaten and to navigate this nocturnal world militated for the evolution of keen senses and disproportionate intelligence. The greatest contribution to perpetuate mammal species thus comes from young, not old individuals, and so the power of natural selection fades with age, making it possible for hazardous late-acting genes to exist.

'Group Selection theory', first proposed by Weismann as early as 1891, proposes that a species benefits by replacing old, worn-out individuals, with younger ones. This concept was refined by Kirkwood to become the 'Disposable Soma Theory', where aging occurs due to the accumulation of damage (physical, and due to genetic mutation) during the lifetime, requiring costly and imperfect repair mechanisms. This gives rise to selection for traits favouring reproductive capacity over bodily (somatic) conservation.

Since natural selection operates less on older individuals it becomes possible for genes that increase survival to reproductive age, or enhance reproductive output early in life, to be selected even if they are associated with negative consequences when older – termed antagonistic pleiotropy. For example, male pattern baldness (or androgenic alopecia) results from hormones essential for fertility causing hair follicles to shrink when older.

Once the dinosaurs disappeared, ca. 65 million years ago, mammals radiated into all available niches, taking with them their evolutionary heritage of low evolutionary pressure on older individuals, mutation accumulation and antagonistic pleiotropy.

So what is Senescence?

We are able to live and function because we have evolved a metabolic process, which takes place in our cells' mitochondria, whereby sugars are oxidised to yield energy. There are, however, by-products of cellular oxidation, 'free radicals', which can cause cell damage and death. As a consequence, cells accumulate oxidative damage (termed free radical damage) over time and senesce. In question is the body's competence to continue to regenerate these cells and to mitigate the damaging effects of 'oxidative stress'. Aging is characterised by a declining ability to achieve high fidelity DNA propagation, to minimise free radical production and to produce antioxidant enzymes that respond to oxidative stress.

Rate of living thus becomes important. Approximately 4% of the oxygen metabolised by mitochondria is converted to free radicals under normal aerobic conditions, therefore a faster basal metabolic rate (characteristic of small r-selected species) generally corresponds to a shorter maximum life-span.

Disease and tissue repair after traumatic damage also affect the rate of cellular division and so the body's ability to produce an effective and efficient immune response enhances survival and longevity.

Badger Life-History: Making the most of the cards your ancestors dealt you

There are many ways in which we humans can live our lives. Some of these options are constrained by circumstances, be these socio-political, gender-biased, resource-based, or resulting from our own genetics (from athleticism to intelligence). Some of our options are also informed by choice, where we define ourselves by our 'place in the world,' our occupation, or our role in society.

This 'freedom' should not be taken lightly, however limited it might be, because it is a step in social evolution not shared by the vast majority of other mammals.

If you are a badger – you are a badger – full stop. You will need to resist parasitic disease in order to reach sexual maturity, breed as soon and as often as you can in order to leave offspring, and compete for this 'fitness' with the other badgers around you. Each day will be motivated primarily by a single objective – to acquire enough food in order to make any of these activities possible, and no matter how ill or down-trodden you may feel, you will have to seek out sufficient food to get you through every day of your life. Our work at the WildCRU badger project has begun to unravel the realities of how badgers achieve (or fail to achieve) the necessary life-history strategies to optimise their individual success, thereby advantaging the population as a whole.

Age specific breeding success

Darwinian 'success' is achieved during a badger's lifespan so long as it leaves viable, breeding descendants. We have recently examined a series of hypothesis predicting how breeding success might vary with age (Dugdale et al. 2011). Variation in reproductive output between individuals may arise from quality differences (The Selection Hypothesis); from differing skills or physiological condition (Constraint); residual reproductive lifespan (Restraint), or from the trade-off between somatic and reproductive investment (Senescence).

From genetic analyses, using 35 micro-satellite genetic markers to look at the reproductive output of the 502 candidate mothers and 612 candidate fathers marked between 1987 and 2010 (Annavi et al. in prep), we have found that only 228 females (45.42%) and 201 males (32.37%), recruited into the adult breeding population bred successfully. Over an individual's life-span we discovered an initial improvement in breeding success with age, peaking at 5

years in males and 3 years in females, and decreasing with old age, followed by a later and steeper rate of reproductive senescence in male than in female badgers (Dugdale et al. 2011). Breeding success was skewed within age-classes, which was partly attributable to differences in individual quality (Selection Hypothesis). Individuals with a late age of last breeding showed a concave-down relationship between breeding success and experience (Constraint Hypothesis). We found no evidence of abrupt terminal effects; rather, individuals showed a concave-down relationship between breeding success and residual reproductive lifespan (Restraint Hypothesis), with an affect of age of first breeding only in female badgers.



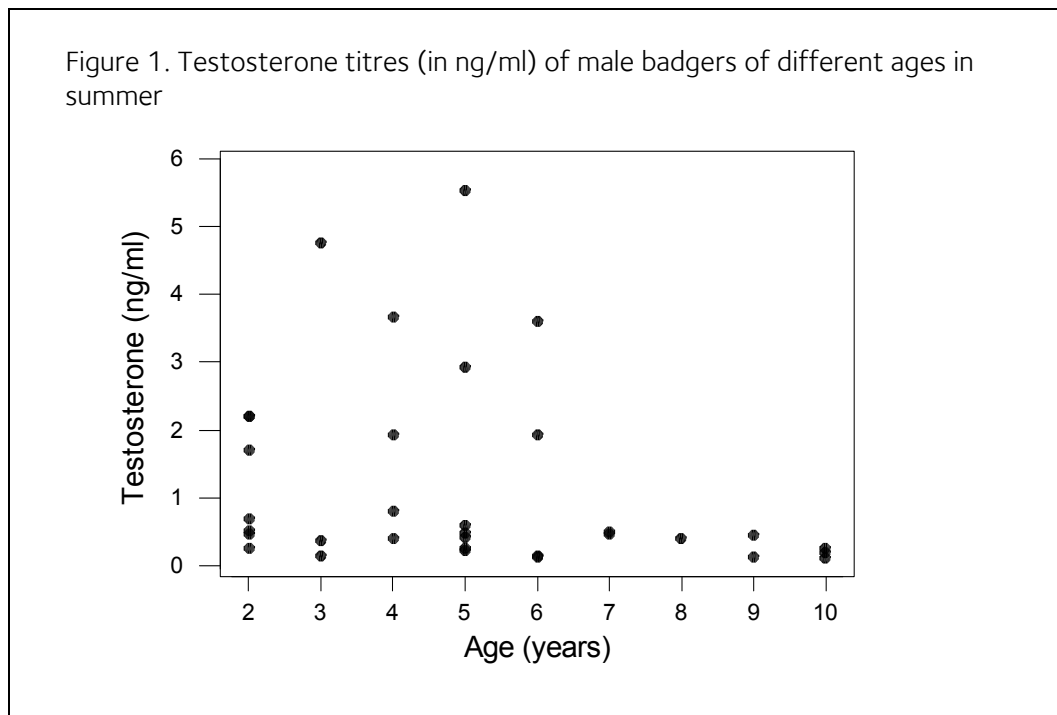
Left: DPhil Student, Geetha Annavi, in the Sheffield University Molecular Genetics Facility (collaborators with WildCRU). Right: A 14 year-old badger scavenging food in Wytham Woods (only 1% live this long: 50% mortality occurs by age 2; 90% by age 8).

We have also observed two endocrinological phenotypes among males (Buesching et al. 2009) – essentially those extending testicular activity into the autumn and those conserving reproductive effort with mid-summer testes ascent. With regard to life-history strategy, it proves interesting that all males over the age of six adopted the conservative strategy (Figure 1), indicating that males either switch phenotypes with senescence or that extended testicular activity results in lower life expectancy, evidencing the costs of reproduction in male badgers, where sustaining testicular activity later into autumn correlates with more bite wounds and anaemia.

Developmental asymmetry & Antioxidant ecology

Of those cubs born to that less than 50% of the adult population that breed successfully, the first crucial life-history test they face is surviving adolescent challenges, with implications for the composition of the next generation of the population.

We have noted that parasitic infections have serious consequences for juvenile survival in badgers, so much so that badger cubs suffering from the highest intensity of endo-parasitic infection grow up to be relatively more asymmetrical than their less severely infected contemporaries (Nouvellet et al. 2011). Such 'Fluctuating Asymmetry' results from the inability of individuals to buffer their development from environmental stresses.



Our most recent work is demonstrating that the mechanism underlying this ability to respond to stress is connected to the ability of juvenile badgers to resolve the reactive oxygen species (free radicals) generated by infection, tissue damage and catabolic metabolism (Bilham et al. subm). We have found that, despite immaturity, cubs (ca. 16 weeks old) already exhibit antioxidant capacity equivalent to those of prime-age adults (1-5 years old). Compared to individuals aged 6 years and over, cubs exhibit significantly higher total plasma antioxidant capacity (Figure 2).

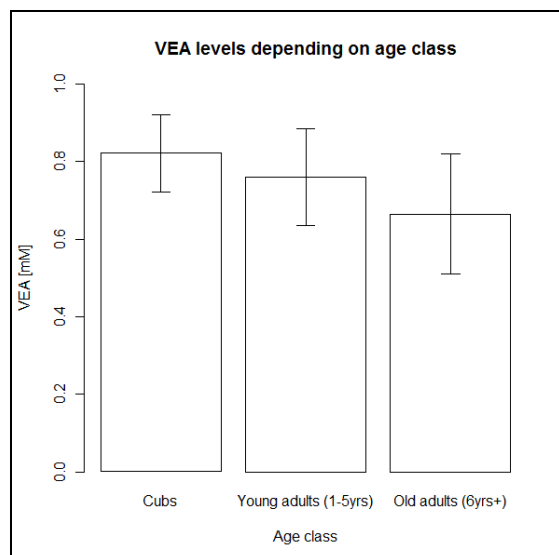


Figure 2. Total plasma antioxidant capacity expressed as vitamin E analogue (VEA) equivalent units (mM / ml plasma) for cubs (n=12) young adults (n=39) and old adults (n=15). Plots show the mean and standard deviation for each category.

Antioxidant systems are extremely costly to implement, where energy would alternatively be invested in growth and development (Montes et al. 2011). Most taxa, therefore, exhibit conservative development of antioxidant systems, in what has been posited to be an evolutionary trade-off. That badger cubs do not fit the typical ontogenic pattern underscores the intensity of selection – through differential mortality – for the antecedence of rapid antioxidant capacity development as a life-history imperative. Simultaneously, the decline in antioxidant capacity in older badgers fits with the free radical theory of ageing.

Our latest research is also looking at the evolution and function of the badgers' immune system. The Major Histocompatibility Complex (MHC) is of particular interest to the study of evolutionary genetics owing to its special pattern of molecular evolution. MHC is a diverse gene family that plays a crucial role in the vertebrate adaptive immune system and in auto-immunity. Greater MHC diversity permits greater antigen presentation to infectious challenges (Sin et al. in press), and is achieved through advantageous mating, where certain pairings will result in superior offspring. We are now looking at mating success in the context of resistance to parasitic infection (Sin et al. in prep). Indeed, it is thought that this ability for individuals to recognise their optimal mating counterpart, with whom to maximise MHC heterogeneity, may be based on olfactory cues, and given our previous research looking at the role of olfaction in badger society this is something we are currently pursuing (Sin et al. subm).

Optimisation under conditions of uncertainty: Climate Change

Our work on the Badger Project has long-since established a link between badger population success and climatic conditions (Macdonald & Newman, 2002; Macdonald et al. 2010). Climatic conditions are a defining element in the evolution of optimal life-history strategy, that is selection for a bounded range of seasonal temperature and humidity maxima and minima to which a species' physiology is adapted and its behaviour optimised. Our latest research has discovered that badger life-history optimality is linked strongly not just to absolute climatic variables, but also to the variability in weather patterns (Nouvellet et al. subm).

Using multi-model inference (Akaike) procedures, we have been able to decompose yearly temperature and rainfall into mean trends, yearly amplitude of change and residual variation, using daily records for the Oxford area (Nouvellet et al. subm). We have detected a significant trend in mean temperature, equivalent to a rise of 2°C since 1881. However, no significant long-term trend was apparent for seasonal temperature amplitude, or for yearly residual standard deviation. Annual mean rainfall also increased significantly with time, but we found no significant long-term trend in the coefficient of variation of rainfall.

Based on 1,125 badger life histories (from 1987 to 2008) we found that annual mortality and recruitment rates both responded to changes in mean trends and to variability in proximate weather components. Mean adult survival rate (81%, SE 0.01) was higher than juvenile survival rate (67%, SE 0.03) in this analysis (Nouvellet et al. subm), which concurs with previous studies (Macdonald et al. 2009; 2010).

Mean daily rainfall proves to be the most influential predictor; its relative influence was more than three times higher than that for any other predictor. Low adult survival was associated with only the driest, and not the wettest, years, while for juveniles optimum survival was associated with intermediate rainfall. Rather than finding trends for population dynamics to increase as a linear response to weather variable, however, we established that both juvenile and adult survival rates were highest when variability in temperature was close to its mean value over the study period. Juvenile survival and recruitment also benefited from intermediate levels of mean rainfall and was highest during years with lower amplitude of temperature change between winter-summer.

For cub recruitment (a measure of population productivity), all weather metrics had relative high influences, revealing that the most supported Akaike models contained many climatic covariates. We deduce that modelling recruitment is linked with weather more intricately than modelling survival rates. An optimal range of mean rainfall was again evident, beyond which drier or wetter conditions appeared to be detrimental for recruitment. A similar interaction linked recruitment with the amplitude of seasonal change, with optimal recruitment associated with intermediate amplitude.

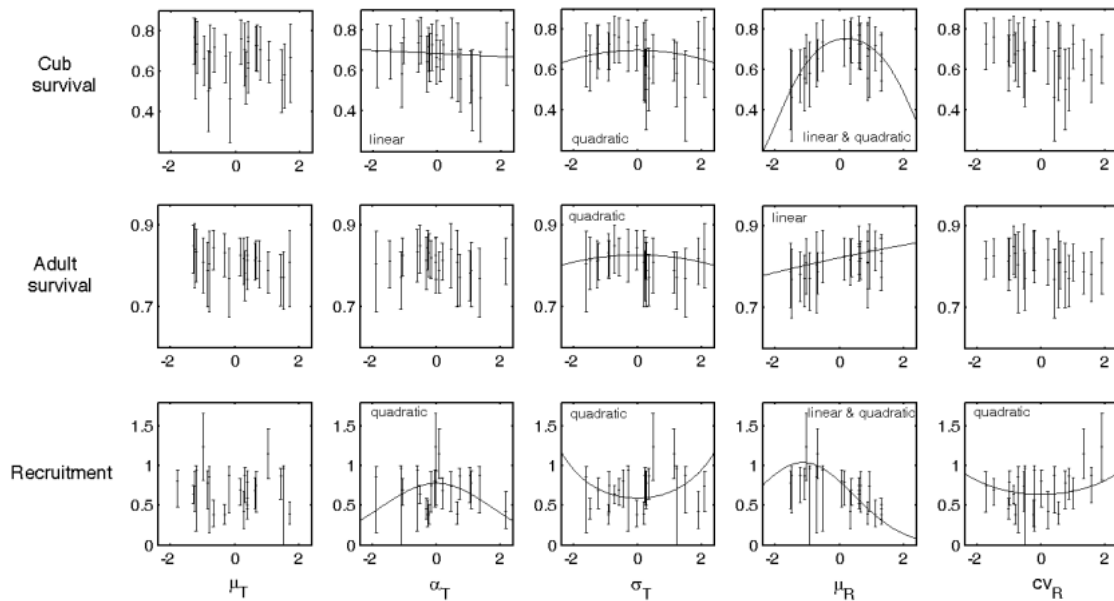


Figure 3. Survival rate estimates for cubs and adults, and recruitment as a function of the climate metrics defined. Estimates of survival rates and recruitment together with their 95% confidence intervals (error bars) are based on model averaging. Solid curve represents statistically significant link between life-history parameters and climate metrics. For each significant relationship, we indicate whether the linear or quadratic (or both) component(s) was (were) significant(s). Importantly, a significant linear component does not imply a straight line in the shown representation as the relationship is defined as linear within a logistic transformation (for survival rates) or within a log transformation (for recruitment).

The benefits of this optimal range – or ‘Goldilocks Zone’ (see Nouvellet et al. subm; ‘porridge’ neither too hot, nor too cold, but just right ~ in the book by Robert Southly) – illustrates that both juvenile and adults exhibit a range of tolerance for residual standard deviation around predicted values, beyond which survival rates declined. Badger life-history parameters, annual routines and capacity to make effective behavioural decisions are thus predicated upon a stable range of climatic conditions, which result in optimal survival and recruitment dynamics.

Conclusions

The evolution of life-history strategies, to maximise reproductive output in the light of impending senescence, are not only fascinating but central to any synthesis in our understanding of evolutionary ecology. Moreover, how increasing unpredictability in climatic conditions influences life-history optimality adds greater impetus to gaining a fuller appreciation of the mechanisms involved.

The long-term nature of the WildCRU’s Badger Project and the unprecedented depth of data we now have at our disposal (largely thanks to support from the PTES) grant us privileged insight into this subject, enabling us to almost see the workings of nature.

So remember, while those annoying grey hairs are in response to glutathione antioxidant deficiency, exacerbated by stress and senescence, they tell an incredible story about the evolution of mammals and our place in this world.

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