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Morphology, Evolutionary History, and Ecology of Neofelis nebulosa as it Relates to Conservation: A Literature Review

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INTRODUCTION

In the beginning of conservation, predators were often managed against as they were seen as dangerous and a factor in the decline of other species, often those valued for game. Recently, however, conservationists have begun to research and understand the importance of apex predators on the trophic interactions within an ecosystem. Experiments done in Yellowstone National Park have highlighted the importance of apex predators, such as the cougar and gray wolf, to maintain a healthy balance between predators, prey, and habitat (Ripple et al. 2015).

This review turns the focus to a less well-known predator, the Clouded Leopard (*Neofelis nebulosa*). This unique species is an important predator in many ecosystems throughout its range, as well as exhibiting unique characteristics that offer important information in the fields of evolution, cladistics, morphology, and behavior. Compared to other members of the Felidae family, *N. nebulosa* has relatively little information known about it. This paper seeks to analyze and understand current information on the biology, ecology, and evolutionary history of *N. nebulosa,* as well as discuss future research that could be done based on missing information.

BIOLOGY

MORPHOLOGY

N. nebulosa is named for is unique cloud-like pelage pattern, containing black-edged ellipses and occasional black spots. The background pelt color is generally lighter than the color within the ellipses (Nowell & Jackson 1995). It is a medium-sized felid, averaging between 11 and 20 kg (Grassman et al. 2005). Its legs are relatively short compared to its long (up to 80-90 cm) body, with the black-ringed tail being equally as long (Nowell & Jackson 1995). The short legs are paired with even shorter forelegs and large front feet, which can create a "spoon shape" when gripping branches (Hubbard et al. 2009). The cranial morphology of *N. nebulosa* is particularly unique, having the largest tooth-to-body ratio (Figure 1) of the extant members of the Felidae family (Hubbard et al. 2009). They have also been referred to as “tapering headed cats” due to the shape of the skull (Sicuro 2011).

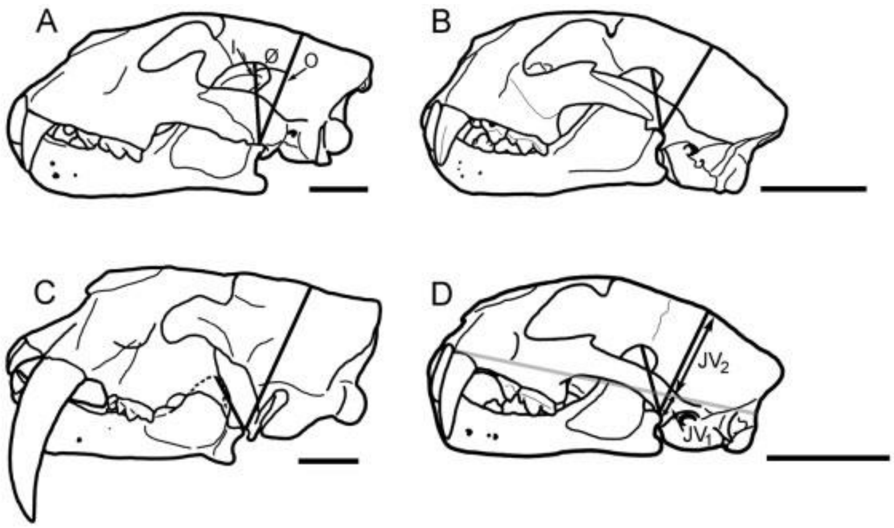

Figure 1: Comparison of “skulls of (**A**) lion (*Panthera leo*); (**B**) puma (*Puma concolor*); (**C**) *Smilodon populator*; (**D**) clouded leopard (*Neofelis nebulosa*) BM3.9.336. Scale bars _ 5 cm.” (Christianson, 2006)

BEHAVIOR AND REPRODUCTION

While the morphology of *N. nebulosa* has been examined from many angles, the behavior and diet of the species receive less attention. Much of what is known about the wild behavior of the species is speculation based on captive observation or has only a few studies supporting it. Ngoprasert et al. (2012) found that *N. nebulosa* density was closely correlated with Reeve’s Muntjac (*Muntiacus reevesi*) and Eurasian Wild Pig (*Sus scrofa*) in a Taiwanese study. Another study associated *N. nebulosa* with smaller prey, regardless of the species’ ability to take down prey of equal or greater mass than themselves. They found evidence of hog deer

(*Axis porcinus)*, slow loris (*Nycticebu*s), bush-tailed porcupine (*Atherurus africanus*), Malayan pangolin (*Manis javanica*), and Indochinese ground squirrel (*Menetes berdmorei*) being part of *N. nebulosa* diet through scat collection (Grassman et al. 2005).

The reproductive patterns of *N. nebulosa* are often researched due to their importance in growing population sizes. Very little is known about reproduction in the wild due to the species' elusive nature. Captive breeding, on the other hand, offers various insights into why this species might struggle to maintain or increase populations. Females become sexually mature at about 2 years old. They experience a long estrous cycle, 15-40 days, with a 4-6-day estrus (Brown 2011). Males have very low sperm quality (Pope et al. 2010). This low quality complicates reproduction, as does intraspecies aggression (DeCaluwe et al. 2013). The intraspecies aggression is mainly caused by anxiety and stress in captive animals, which has been measured by fecal corticoid concentrations (Wielebnowski et al. 2002), fAM levels, and keeper questionnaires (DeCaluwe et al. 2013).

EVOLUTIONARY HISTORY

The uniqueness of this species, in the eyes of evolutionary analysis, puts an exceptional importance on its conservation and allows for research that could potentially shed some light on past interactions. Evolutionary research regarding *N. nebulosa* falls into several categories: understanding where *N. nebulosa* is in relationship to other extant felids, understanding the relationship of *N. nebulosa* to extinct saber-tooth species, and understanding the differences within the *Neofelis* genus.

For many years, *N. nebulosa* was considered a "large-small" cat based on its small size but shared characteristics with the pantherines. Christiansen (2006), however, concluded that this classification was entirely wrong and that *N. nebulosa* is too unique to be classified amongst small and large cats. This unique set of characteristics has placed *N. nebulosa* as a “basal pantherine”, or as the sister taxa to the genus *Panthera* (Christiansen 2008a). Further research considered if this distinctiveness was caused by a shared ancestor of extinct saber-toothed felids. Surprisingly, researchers could find no such evidence. Morphologically, the uniquely large canines and the large gape of *N. nebulosa* did hint at ancestral ties to extinct saber-toothed species. Andersson et al. (2011) found, however, that, though the species had the largest gape, it shared a gape angle with many on the extant felids. This combined data places *N. nebulosa* as an “intermediate” between nonsaber-toothed and saber-toothed felids (2011). Christianson et al. found similar results in 2006, stating that *N. nebulosa* shared characteristics of some of the less derived extinct saber-toothed species. This unique morphology continues to stump researchers as they attempt to classify *N. nebulosa* correctly. Currently, there is some debate that *N. nebulosa* may be the ancestor of a new saber-toothed radiation (Therrien 2005) and is experiencing accelerated evolution compared to other extant felids (Yu and Zhang 2005).

This accelerated evolution theory is supported by research into species and subspecies level divisions within the *Neofelis* genus. Though now widely considered incorrect, the original classification included one species, with four subspecies within *N. nebulosa*: *N. n. macrosceloides* in India, Nepal, Sikkim, and Bhutan; *N. n. nebulosa* in SE Asia and China; *N. n. diardi* in Sumatra and Borneo; and *N. n. bracyura* in Taiwan, (Buckley-Beason et al. 2006, Kitchener et al. 2006) as outlined in Figure 2. It is noted that a study done more recently in Taiwan deemed *N. n. bracyura* extinct (Chiang et al. 2012).

However, recent cranial and dental morphological (Christiansen 2008b), pelage morphology (Kitchener et al. 2006), and molecular (Buckley-Beason et al. 2006) evidence shows that there are two distinct subspecies, *Neofelis nebulosa,* and *Neofelis diardi.* This is the currently the most widely accepted status. It is unknown if the Taiwanese population was, in fact, a distinct subspecies, a distinct species, or a member of the mainland species. Though most agree upon leaving the division at two species, Wilting et al. (2007) furthered this idea by suggesting that *N. diardi* is divided into two subspecies, separated into the islands of Borneo and Sumatra. He stated that the geographic isolation of these islands has caused two distinct genetic populations.

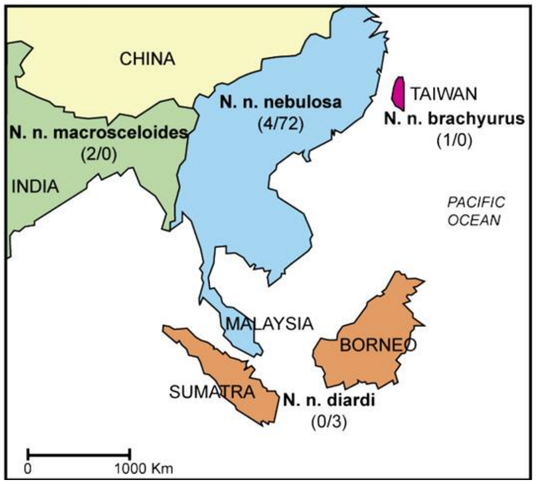

Figure 2: Geographic range of the four predicted clouded leopard subspecies (Buckley-Beason et al. 2006)

Evolutionary studies aid us in conservation by giving us the most accurate idea of what species are and what their relationships are to others. By understanding that a species is instead made up of distinct subspecies or in fact two unique species, we are better able to preserve the unique genetics of each group. In keeping in line with this, it is noted that much of the research being analyzed here is focused on the mainland clouded leopard, *Neofelis nebulosa*, under the assumption that it consists of one species with no subspecies, as most research assumes.

ECOLOGY

Understanding the habitat in which *N. nebulosa* occupies is crucial in understanding relationships between *N. nebulosa* and other species. The range of *N. nebulosa* extends through much of Asia and is found in the Himalayan foothills potentially up to 3000 feet, in Burma, Thailand, South China, India, Nepal, and the Islands of Borneo and Sumatra, as shown in Figure 3 (Nowell & Jackson 1995). It was originally found in Taiwan but is now believed to be extirpated from the area (Chiang et al. 2012). In each of the areas that the species is located, the habitat has some variation, which makes it very difficult to understand what ideal habitat for the species is. However, by comparing the habitat in several study areas, we can use commonalities to hypothesize a best-fit habitat. In Thailand, the species was found in three distinct habitat types: closed forest, open forest–grassland, and abandoned orchard (Grassman et al. 2005). It is most often found in primary evergreen tropical forests (Nowell & Jackson 2005), but evidence has shown that logged forests are also valuable (Mohammed at al. 2015). Elevation is also critical to distribution; *N. nebulosa* is traditionally observed in slightly higher elevations. One study observed individuals between 90 and 1253 meters (Ngoprasert et al. 2012). The home range size of males and females do not differ amongst each other but do vary from 22.9 to 51.0 km^2, with moderate intersex and intramale overlap, as shown in Figure 4 (Grassman et al. 2005).

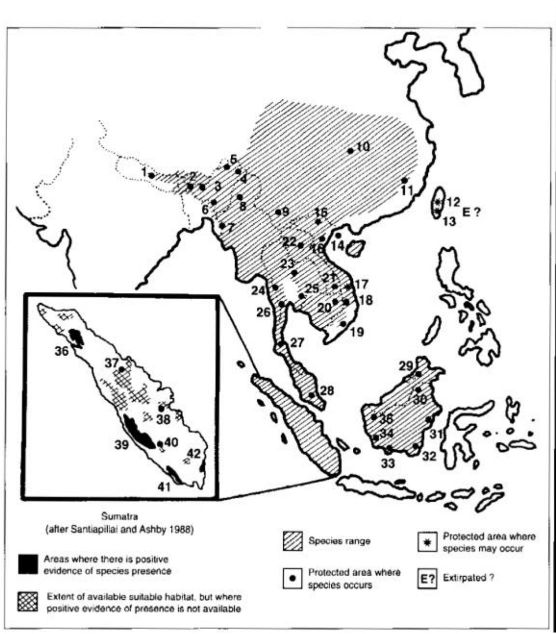

Figure 3: “Distribution of the clouded leopard (*N. nebulosa*).” (Nowell & Jackson, 1995)

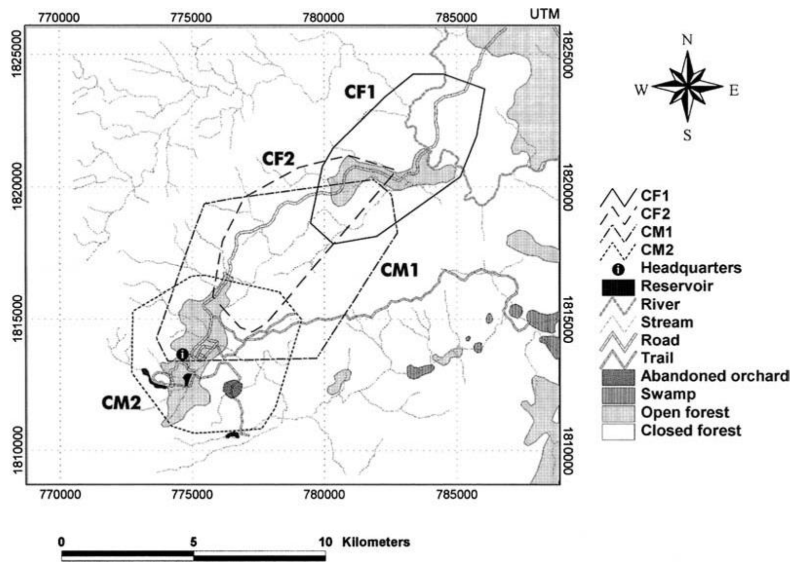

Figure 4: “Clouded leopard annual ranges (95% minimum convex polygon estimator) in Phu Khieo Wildlife Sanctuary, Thailand (April 2000 to February 2003).” (Grassman et al. 2005)

The importance of habitat, therefore, doesn't necessarily lie in the type of forest, but in what qualities the forest offers for the everyday lives of members of the species. *N. nebulosa* is a solitary species, except for adult females with young (Padmanaba et al. 2013). They are mostly nocturnal and very cautious of humans (Padmanaba et al. 2013). They are partly arboreal, and though they do not spend their entire lives in trees as once believed, they will often use trees for hunting and rest, and they show remarkable skills when it comes to navigating the arboreal landscape (Chiang et al. 2007). They are observed in open grasslands at night, normally hunting, but require closed forests for denning (Grassman et al. 2005). From the assessed information, a suitable habitat can, therefore, be deduced. *N. nebulosa* needs a space large enough to support their solitary life, ideally, patches greater than 40 km^2, or as groups of patches with a total area of 40 km^2 that are within 1 km of each other (Chiang et al. 2007). The habitat should be in a partially closed forest, so that denning females have access to both protection for cubs and open grassland for hunting, and have habitat for abundant moderate-sized prey.

N. nebulosa is marked as Vulnerable throughout its entire range, and extinct in Taiwan (Nowell & Jackson 2005). Ecological information about the species is crucial in understanding what can be done to improve the status of the species as a whole. Beyond habitat association, it is also important to understand associations with other species. *N. nebulosa*, where still present, has varying and important roles within the ecosystems it inhabits. For example, In Taiwan before extinction, *N. nebulosa* was the apex predator. Since its disappearance from the island, many of the herbivorous species assumed to have been prey to *N. nebulosa* have increased in number (Chiang et al. 2007, Chiang et al. 2012). The lack of predation, exacerbated by restricted hunting, has caused a trophic release, allowing the previously hunted species to flourish. So far, there is no evidence that the local environment has not been negatively affected by this (Chiang et al. 2012). However, loss of apex predators for extended periods of time has been known to cause trophic cascades, where the release of the secondary consumers causes an equivalent loss in primary producers. This was seen in the loss of the cougar and gray wolf in Yellowstone national park and was remedied with reintroduction (Ripple et al. 2015). Further research is necessary to understand if locations, where *N. nebulosa* have been extirpated, face the same threat.

Other ecosystems, however, contain multiple carnivores that *N. nebulosa* interacts and co-habitats with. Experiments done in Manus National Park in India suggested that *N. nebulosa* was sympatric with tigers (*Panthera tigris*) and leopards (*Panthera pardus*) (Borah et al. 2014). The same thing was found in Thailand, showing sympatry with the Asiatic golden cat (*Catopuma temminckii*) and the marbled cat (*Pardofelis marmorato*) (Grassman et al. 2005, Jenks et al. 2011). An even broader study expanded this data throughout Asia, concluding that *N. nebulosa* was sympatric with most small cat species it cohabitated with, compensating for the overlap with nocturnal ground movement at night, and arboreal movement during the day (Lynam et al. 2013).

This realization that *N. nebulosa* is not in danger of being outcompeted, nor is it a competitor to other species, does offer some support to the idea that *N. nebulosa* will not receive backlash in the conservation of other species, at least not that of other carnivores. This research allows us to understand that habitat and prey abundance are keystones in *N. nebulosa* conservation, and competition is not.

MISSING INFORMATION

Researchers of this unique species are constantly trying to gather more information to help piece together exactly what *N. nebulosa* is, and what its importance to science may be. To further aid in the conservation effort of *N. nebulosa*, more research is necessary to understand what exactly needs to be done. Though we know quite a bit about the morphology of the animal, little is still known about how the animal operates in the wild. We still know very little about topics such as preferred prey and breeding outside of captive populations. It is also necessary to gather further information on habitat to continue to specify what habitat is crucial for the survival of the species.

Though the current status of *N. nebulosa* is a basal pantherine, further research is also needed to understand exactly the relationship between *N. nebulosa* and other felids, as well as the relationship of the different populations of *Neofelis*. More research is also necessary to understand what, if any, negative effects Taiwan may face in the absence of its apex predator, and what, if any, threats there are to current populations.

REINTRODUCTION INTO TAIWAN

Without action, the status of *N. nebulosa* will continue to decline. In the past, reintroductions have been used to rescue many species from extinction, and have been done successfully in apex predators, such as the grey wolf (Ripple et al 2005). *N. nebulosa* has been extirpated from Taiwan, but studies have shown that there is viable habitat on the island that could be used as a reintroduction site for the species (Chiang et al 2012). Before action is taken, however, a comprehensive look at all the factors of a reintroduction process must be evaluated. A location must be studied and evaluated for availability of viable habitat, including space, food, and shelter. A reintroduction method must be established, as well as a population in which to pull from. A protocol for post- introduction monitoring must also be evaluated to ensure that the reintroduced population grows.

HABITAT

To assess where in Taiwan is best for a reintroduction and management site, one must first consider habitat requirements of *N. nebulosa*. As they are found in many places in Southeast Asia, so they are found in a wide range of habitats. Traditionally, it is believed that they prefer primary evergreen forests, but can also be seen in secondary and logged forests

(Nowell and Jackson 1996). More recent studies have suggested that primary and selectively logged forests provide no significant difference in success (Mohamad et al. 2015). Elevation is critical to distribution; *N. nebulosa* is traditionally observed in slightly higher elevations. One study observed individuals between 90 and 1253 meters (Ngoprasert et al. 2012). However, they are rarely observed up to 3000 meters (Nowell and Jackson 1996). *N. nebulosa* is one of the more arboreal species, and trees that are suitable for resting and hunting are crucial (Mohamad et al. 2015). The home range size of males and females do not differ amongst each other, but do vary from 22.9 to 51.0 km^2, with moderate intersex and intramale overlap (Grassman et al. 2005). Therefore, patches greater than 40 km^2 are deemed as suitable habitat, as well as groups of patches with a total area of 40 km^2 that are within 1 km of each other (Chiang et al. 2007). Area suitability is also highly reliant on the abundance of prey species.

To meet these requirements in Taiwan, researchers have established that the Tawu Mountain area in Southern Taiwan is the most likely habitat for a successful reintroduction. It is the second largest continuous patch of suitable habitat at 2022 km^2 and contains the largest lowland primary forest on the island (Figure 5). This suitable habitat was evaluated based on the type of vegetation, altitude, and distance to disturbances (Chiang et al. 2015).

While the Tawu Mountain area is the most suitable habitat that Taiwan has to offer, the area is far from safe from threats and degradation. The most prominent threat is human encroachment and habitat fragmentation. The area must be actively managed before, after, and during reintroduction to ensure the highest chance of success. Management of the primary forest falls into two categories: ecological management and political management.

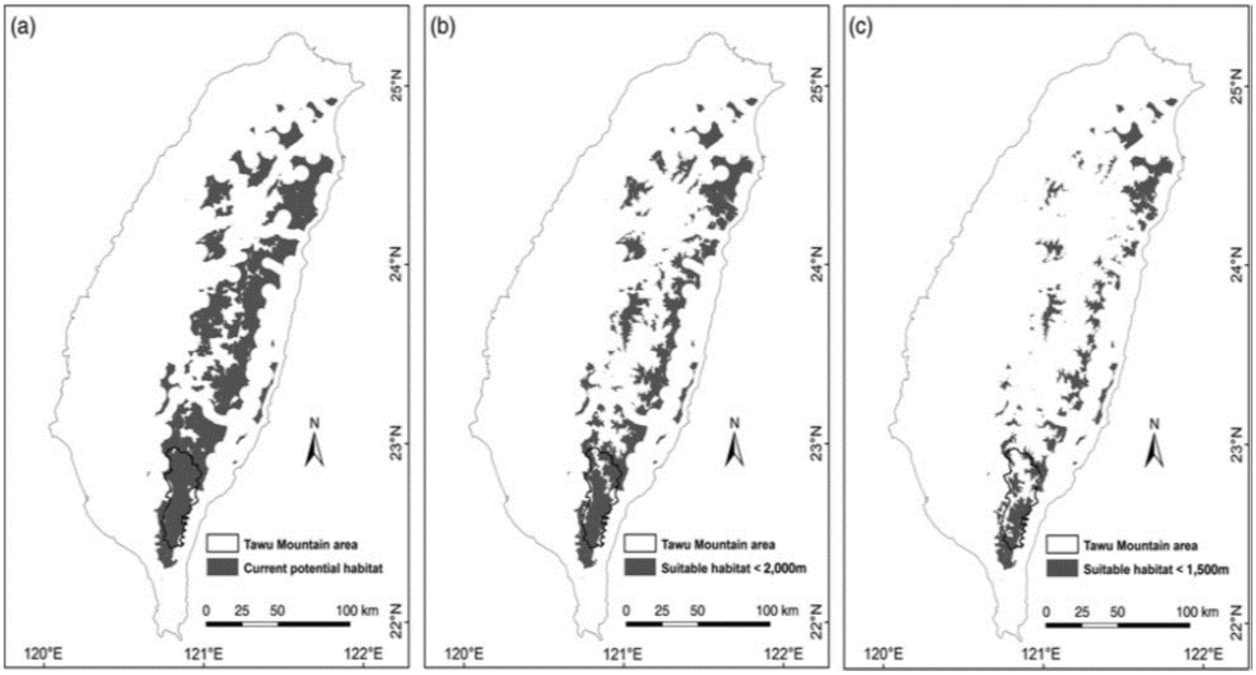

Figure 5: Distribution of suitable habitat for *N. nebulosa* Neofelis nebulosa in Taiwan, excluding areas close to roads and villages, (b) suitable habitat at >2000m altitude, and (c) suitable habitat at >1500 m altitude. Reprinted from: "Is *N. nebulosa* Neofelis nebulosa extinct in Taiwan, and could it be reintroduced? An assessment of prey and habitat" (267), by J.P. Chiang, 2015

Ecological management consists of practical application of old growth forest management techniques. While little is known about exact habitat use of *N. nebulosa*, we do know that they use large trees for resting and hunting (Mohamad et al. 2015). While unconfirmed, it is predicted that *N. nebulosa* either dens in tree hollows (Pratar 1965) or in dense thickets of dead limbs (Grassman et al. 2005). Snag management, therefore, is important. Since the exact habitat for dens is unknown, adaptative management may be necessary and den management may have to change if further information reveals a better den habitat. The Tawu Mountain area is dominated largely broadleaf and mixed broadleaf-conifer forests. While conifer forests are present in the area, they are at higher altitudes than *N. nebulosa*s are typically found, and therefore, are not of concern (Chiang et al. 2015). Because conifers and some broad-leaf species do not naturally form cavities (Hunter 1999) artificial cavities may need to be created. Field measurements will need to be taken to evaluated the abundance of cavities to decided what level of maintenance is necessary. Another maintenance technique that may be necessary is fire or selective cutting to maintain forest gaps and understory if these characteristics are not being maintained naturally. Grassman et al. (2005) also found that there is some use of open grassland, but it is not necessarily required, so if grassland is present, it should be monitored for usage by the reintroduced individuals to understand if it should be a priority in management.

Political maintenance of habitat may be more difficult, as pressure to increase human activity in the area is very high. Threats of a major highway through the forest would cause fragmentation that would likely reduce viable habitat to nearly non-existent (Chiang et al. 2007). Fortunately, this highway production is stalled due to laws prohibiting construction in a nature reserve. However, the project has not been canceled and legislation could potentially allow its creation (Chiang et al. 2007). Further regulations may also need to be put in place to limit hunting and poaching of both prey and predator, as well as regulations limiting access to areas to maintain natural conditions. While the area's status as a preserve prevents and agriculture or housing developement, increased recreational presence could disturb both the environment and the solitary creatures (Chiang et al. 2007).

When understanding habitat requirements, maintenance of prey habitat and numbers must also be considered. The densities of preferred prey species, such as the Formosan serow (*Capricornis swinhoei*), Formosan macaque (*Macaca cyclopis*), and Reeves's muntjac (*Muntiacus reevesi*) (Chiang et al. 2007) are relatively high in this area (Chiang et al. 2012). Continued maintaince can come from two different perspectives, bottom-up and top-down. Bottom-up management involves maintaining ecosystem factors to provide ample resources of prey, while top-down requires management of predators. Currently, Taiwan lacks an apex predator, so top-down management will come with a reintroduction (Chiang et al. 2015). The response of prey to this introduction must be closely managed to ensure proper prey abundance is maintained after reintroduction.

However, bottom-up maintenance should begin before reintroduction to ensure healthy prey populations. Generally, prey abundance is correlated with low human disturbance and low altitudes (Chiang et al. 2015). While altitude cannot be altered, reducing human disturbance will help keep these populations high. Formosan macaques are generally found when there is a "smaller slope, convex terrain, lower heterogeneity of terrain shapes, higher shrub cover, and higher visual obscurity, drier aspect and lower values of canopy cover" (Chiang et al. 2007). While Reeve's muntjac prefers "non-rhododendron forest, gentler slope, lower heterogeneity of tree densities among 3 size tree classes, higher values of canopy cover, and lower canopy height" (Chiang et al. 2007). The Formosan serows were found closer to cliffs and farther from rivers. They, like the Formosan macaque, prefer convex terrain, higher rock cover and visual obscurity, and lower heterogeneity of terrain shapes. Conversely, they prefer lower shrub cover. Like the Reeve's muntjac, they like lower heterogeneity of tree densities among 3 size tree classes. They also prefer "higher basal area, lower large tree height, more tree stratum, and higher heterogeneity of canopy cover" (Chiang et al. 2007).

In summation, because we do not know the exact preferred prey of *N. nebulosa* in Taiwan, we must take an all-inclusive "best fit" management strategy to manage abundance for as much potential prey as possible, then modify actions when further research reveals more specific preferences for prey. In general, however, we can manage for lower heterogeneity of size classes (to a degree). For other values, like canopy cover, shrub cover, and visual obscurity, we must manage for heterogeneity to provide ideal habitat for as much biodiversity as possible. While preparing for reintroduction, selective culling of prey species with large numbers may be required to maintain healthy population levels while there is still an absence of predation.

REINTRODUCTION METHOD

There are several ways in which a reintroduction could be done. Using previous research as a guide will allow for the most successful reintroduction possible. The reintroduced population either needs to be captured from the wild or pulled from a captive population. A wild capture could be difficult due to the elusive nature of the species (Nowell & Jackson 1996), but would offer a population that was adapted to and familiar with the habitat they were being reintroduced to. Due to genetic similarity, this population should be pulled from the mainland species (Chiang et al. 2015).

The other option of pulling from a captive population, which could be easier. The issue with this method is that captive populations have low genetic diversity, and are not acclimated to wild living. For this method to work, a new population would need to be started. Improved facilities would be needed to breed and raise cubs in a controlled environment that allowed for minimal human contact and freedom to gain skills such as hunting. Because of intraspecies aggression (DeCaluwe et al. 2013). the reintroduced population would need to be familiarized as cubs.

Once the individuals were captured, regardless of method, they should be vaccinated for common diseases of the species to ensure optimum health. The individuals should also be radio collared or chipped for monitoring post-reintroduction. This not only will allow us to track the individuals, but will allow for monitor of wild behavior that we currently have no information on. The individuals should then be released, either by a soft release or a hard release.

The method of release that is most likely to be successful would be a soft release, as was done in the extremely successful grey wolf reintroduction (Ripple et al. 2015). This would require a fence to be built that would allow for the individuals to be within the habitat, but isolated in some way. Further research would be needed to be done to understand where in the Tawu Mountain Area the soft release would occur, as well as to predict what the best size of the release are would be, and what time period the release should occur during.

POST-REINTRODUCTION MONITORING

Because so little information is known about predator-prey relations and habitat association of *N. nebulosa*, extensive monitoring before, during, and after introduction is crucial. Data on prey abundance, habitat health, and predator habitat use must all be continuously collected and management techniques modified as new information is attained. Most previous research on the area was done through camera trapping. This method is likely sufficient for prey abundance as radio tracking for all species would be very expensive. Monitoring of clouded leopard scat and kills will give information on what individuals are eating to better know which animals to continue management for or if new management needs to begin for other species. This data will also allow us quantified the amount of predation of each species to predict loss from the prey populations. Continuing vegetation samples should be collected to monitor the sustainability of both predator and prey habitat, as well as for usage of den sites. Most data will come from direct observation of the introduced individuals through the radio-tagging. This tracking can be used to learn if there is a further preference within a habitat, what females prefer for denning and to better collect data on prey. This management-focused reintroduction will not only aid the in the restoration of the complete food chain in Taiwan but will also provide improved knowledge on how to better maintain existing populations in both mainland Asia and on the islands of Borneo and Sumatra.

CONCLUSION

N. nebulosa is extremely important to many aspects of science, including ecology, evolution, and taxonomy. It is still unknown all that the study of this species can tell us. Researchers are constantly searching for more information, and revising current classifications. Throughout the past few years, scientists have discovered that existence of two species of *N. nebulosa*s and gained the understanding that these species may be the beginnings of a new radiation of saber-toothed cats. That knowledge, along with the ecological importance of *N. nebulosa*, highlights the importance of conserving this amazing species.

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