

Zoo (Wahlstedt, 1984). In order to encourage the public to donate money to the project, as well as to arouse their interest, several 'Panda banks' together with information leaflets about the programme have been placed in different parts of the zoo. Our aim is to inform as many people as possible that the zoo is involved in breeding the threatened species of Sweden, and that the offspring produced may well be used in reintroduction programmes in the future. Of the money received, 50% is given to Skansen to help pay for the construction of better enclosures for those species.

ACKNOWLEDGEMENTS

I would like to express my appreciation to Dr P.-O. Palm and Dr H.-O. Larsson at Skansen Zoo, to Dr L. Von Essen of the Swedish Sportsmen's Association and to M. Olsson of the Natural History Museum, Stockholm, for providing valuable information. I also thank E.

Lundberg and V. Olvang for their help in the preparation of the manuscript.

REFERENCES

CORBET, G. B. (1978): *The mammals of the palaearctic region: a taxonomic review*. London & Ithaca: British Museum (Natural History) & Cornell University Press.

KJERNER, I. (1982): Miljögifthotade arter — läget fortfarande kritiskt. *Miljöaktuellt* 10: 8–9.

LARSSON, H.-O. (1984): Överlever fjällräven. *Zool. Tidskr.* 2: 17–19.

MECH, L. D. (1970): *The wolf: the ecology and behaviour of an endangered species*. Garden City, NY: Natural History Press.

OLSSON, M. (1978): PCB and reproduction among Baltic seals. *Riistatieteellisä Julk.* 37: 40–45.

OLSSON, M., REUTERGARD, L. & SANDEGREN, F. (1981): Var är uttern. *Sveriges Natur* 6: 234–240.

PALM, P.-O. (1981): *Project Eagle-owl South-East* (information leaflet). Stockholm: Rädda Berguvan.

VON ESSEN, L. (1984): Projekt fjällgas — et försök att hjälpa en hotad djurart. *Zool. Tidskr.* 2: 13–16.

WAHLSTEDT, J. (1984): Skansens WWF-projekt. *Zool. Tidskr.* 2: 6–7.

Int. Zoo Yb. (1986) 24/25: 192–199

Restoring a wilderness: the reintroduction of wildlife to an African national park

J. L. ANDERSON

Deputy Director, Research, National Parks and Wildlife Management Board, Private Bag X2078, Mafikeng 8670, Bophuthatswana, South Africa

In most parts of the world today it is almost impossible to secure new areas for conservation where the land, vegetation and wildlife have not already been subjected to change by man and his livestock. In southern Africa the existing network of conservation areas must be expanded if all the major veld types, as described by Acocks (1975), and many critical habitats are to be represented in the future. Virtually all the conservation areas proclaimed in southern Africa since 1970 have been previously settled and their wildlife populations considerably reduced. These areas have required varying degrees of management for their restoration to what is considered as near as possible their original

state. The Pilanesberg National Park in Bophuthatswana, South Africa, is an example of such an area.

BACKGROUND

Pilanesberg is an extinct caldera of four concentric cones, which are about 1000 million years old and heavily weathered, intersected by 16 major drainage lines which radiate out of the mountain. The area covers c. 50 000 ha, the predominant vegetation type is sour bushveld and the mean annual rainfall is 630 mm. Numerous old kraal sites (large, usually circular, fenced-in areas containing living quarters and livestock enclosures) indicate that the area was used as grazing land

from about the 14th century. The impact of these early human settlements can never be assessed but many of the worst eroded areas are associated with old cattle kraals. Within the last 200 years the area was settled by a pastoral people, the Batswana, and towards the end of the 19th century European settlers established farms in the area and cattle ranching with some maize production was further developed. Particularly during this last period of settlement changes had been effected on the vegetation as a result of cultivation and overgrazing by livestock as well as of fire. At the same time the diversity and numbers of larger mammals had been drastically reduced.

With the formation of Bophuthatswana and the granting of self government, title to the large privately owned farms reverted to the State and it was considered that, in the national interest, the Pilanesberg area should become a game reserve rather than remain under livestock. Alternative land, together with financial compensation, was provided to those citizens who still lived in the area and the park was proclaimed a national park in November 1979.

Pilanesberg is being developed with four main objectives:

1. To conserve the ecosystem in as natural a state as possible;
2. to provide a base from which a sustained yield can be obtained from the natural resources of the area, the benefits of which will go to the people living adjacent to the reserve;
3. to use the reserve as a centre for environmental education in Bophuthatswana;
4. to provide aesthetic, spiritual and recreational enjoyment for visitors while at the same time maintaining public use to a level where it is compatible with the other aims.

RESTORATION PROCESS

The restoration process began with two broad plans of action: first, the removal and repair of the signs and results of human occupation, although Iron Age sites are considered to be of historical value and are therefore preserved, and second, the reintroduction of wildlife known historically to have occurred in the area. Concurrent with these aims

was the development of the infrastructure required for a proposed national park such as a perimeter fence, staff accommodation, a road network and visitor facilities. Since there is no information available to indicate the kind of plant life which originally grew in the area, management is aimed at controlling erosion and maintaining the diversity of most of the existing vegetation.

RECLAMATION

The removal of cattle fences, because of their potential hazard to wildlife, was the first priority in the reclamation programme. With the help of voluntary workparties some 500 km of barbed-wire fences were removed and the materials donated to the local people. The next step was to remove plants which were considered to be alien to the area, such as *Eucalyptus* spp and *Melia azedarach*, since, although such plant-life has not been shown to pose a serious ecological threat, its presence does not accord with the primary objectives of the park and also it detracts aesthetically from the natural vegetation in the area. Both mechanical means and selected aboricides have been used and while the majority of alien trees have now been successfully removed it will be a number of years before all have been eradicated because regeneration and dormant seeds will provide new growth. A further necessity was the removal of over 120 buildings, including several large houses and two schools; these were demolished and the rubble was either buried or used to fill erosion gullies. Methods of controlling soil erosion have been tested for the most cost-effective strategy under the prevailing circumstances.

REINTRODUCTION OF WILDLIFE

Ideally the steps involved prior to any reintroduction are (1) taking a census of the wildlife already present; (2) conducting research into what species occurred formerly; (3) establishing a policy and principles for selecting the species to be reintroduced; (4) determining the carrying capacity of the area and the proportions of each species to be stocked. Given the circumstances, however, we were unable to conduct the first two steps

with any degree of accuracy and proceeded to establish a policy for species selection, discussed in detail by Collinson & Anderson (1984).

The carrying capacity on which the initial stocking was based (Farrell & van Riet, unpubl.) was later revised to a more conservative level by Collinson & Goodman (1982). This latter figure of one animal unit (AU) per 15 ha (where one AU is equal to one 456 kg animal) is set deliberately at below that expected from the calculated annual rainfall/metabolic mass relationships (Coe *et al.*, 1976) because the condition of the range available to the wildlife had suffered from excessive grazing by livestock and therefore the pre-set carrying capacity was below the potential.

The most important consideration when stocking any multispecies community is to decide what proportion of each species should be contributed to the total stock. Collinson & Goodman (1982) recommend that the stocking rate is allocated into herbivore feeding classes with each class being represented in specific ratios (Table 1).

A total of 5965 animals from 20 species was introduced into the park between November 1979 and August 1984. All the introductions have been carefully monitored and studies are still under way. An annual census is taken, using a helicopter, and ground sampling is done in late summer and again at the end of winter to establish population age/sex structures and to obtain a visual impression of the animals' general physical condition (Riney, 1955). Concurrent monitoring of the vegetation with an emphasis on its utilisation by herbivores takes place to assist in the refinement of stocking levels. As can be seen from Table 2, results of these monitoring procedures show that by August 1984 16 species were successfully established, one had been unsuccessful, the future of two was uncertain while that of one was optimistic. All known deaths, and the probable causes, are also shown in Table 2. The Black rhinoceros *Diceros bicornis* introduction was given the most intensive monitoring because of the species' endangered status; each animal was fitted with a radio transmitter and its

adaptation to the area studied (A. K. K. Hillman, pers. comm.). The African elephant *Loxodonta africana* release, however, received less attention since the main concerns here were, and still are, that some of the young animals might be unable to fend for themselves and the larger ones might try to break through the perimeter fence.

PROBLEMS EXPERIENCED

Inappropriate species Although historical records indicate that the Pilanesberg area was within the range of the Gemsbok *Oryx gazella*, which was introduced in June 1980, it now appears that the area is no longer suitable for their long-term survival since for two years after the release very few calves were recorded and the general condition of the animals appeared poor. It is possible that the previous populations of Gemsbok occurred in the area on only a seasonal basis or that the vegetation has changed to such an extent that it no longer provides the antelope with an adequate diet.

The introduction of the Cheetah *Acinonyx jubatus* must be considered inappropriate not because the species failed to establish itself but because it was too successful. The six animals released into Pilanesberg had increased to 17 within a year. The impact of their predation became unacceptably high and their numbers were therefore controlled. Cheetah are known to have occurred in the area formerly, and sporadic sightings are still made within a radius of 100 km of Pilanesberg, but it appears that in the absence of the Lion *Panthera leo* and the Spotted hyaena *Crocuta crocuta* the species attains unnaturally high densities (Anderson, 1984). This has been the experience in two other game reserves in South Africa: Suikerbosrand in the Transvaal and Itala in Natal.

Disease susceptibility Pilanesberg lies within the endemic range of the rickettsial tick-borne disease Heart-water (*Rickettsia ruminantium*). Most southern African ungulates are immune to the disease but Springbok *Antidorcas marsupialis* introduced from an area outside its endemic range contracted it and died within a few weeks of being released. A

SPECIES/FEEDING CLASS	NO. AU ¹ PER INDIV.	RECOMM. AU STOCKED	RECOMM. NO. STOCKED	PROPORTION ALLOCATED
Grazers (tall grass of moderate quality)				0.45
Common zebra				
<i>Equus burchelli</i>	1.86	269	500	
Southern white rhinoceros				
<i>Ceratotherium s. simum</i>	1.41	488	200	
African buffalo				
<i>Syncerus caffer</i>	1.01	446	450	
Common waterbuck				
<i>Kobus ellipsiprymnus</i>	2.19	68	150	
Roan antelope				
<i>Hippotragus equinus</i>	1.73	97	170	
Sable antelope				
<i>H. niger</i>	1.97	102	200	
Grazers (short grass of high quality)				0.20
Warthog				
<i>Phacochoerus aethiopicus</i>	5.68	18	100	
Common reedbuck				
<i>Redunca arundinum</i>	5.25	38	200	
Mountain reedbuck				
<i>R. fulvorufula</i>	8.11	49	400	
Gemsbok				
<i>Oryx gazella</i>	2.30	43	100	
Blue wildebeest				
<i>Connochaetes taurinus</i>	2.14	187	400	
Cape hartebeest				
<i>Alcelaphus buselaphus caama</i>	2.64	249	650	
Tsessebe				
<i>Damaliscus lunatus</i>	2.91	69	200	
Mixed (graze and browse)				0.20
Ostrich				
<i>Struthio camelus</i>	4.17	24	100	
African elephant				
<i>Loxodonta africana</i>	0.36	140	50	
Eland				
<i>Taurotragus oryx</i>	1.25	304	380	
Impala				
<i>Aepyceros melampus</i>	6.20	160	1000	
Springbok				
<i>Antidorcas marsupialis</i>	8.11	25	200	
Browsers				0.15
Black rhinoceros				
<i>Diceros bicornis</i>	0.65	47	30	
Giraffe				
<i>Giraffa camelopardalis</i>	0.69	218	150	
Greater kudu				
<i>Tragelaphus strepsiceros</i>	2.48	222	550	

¹AU: animal units (equal to 456 kg body weight).

Table 1. Herbivore species stocking rate guidelines for the Pilanesberg National Park, South Africa (after Collinson & Goodman, 1982).

SPECIES	NO. RELEASED		PROBABLE CAUSE	REMOVALS 1981-AUG 1984	STATUS AUG 1984	CONCLUSIONS
	NOV 1981- AUG 1984	NO. DEATHS				
Ostrich	37	0		1	60	successful
Cheetah	6	0		10	?	special case
African elephant	50	6	age/social		44	optimistic
Common zebra	679	17	release condition/ social	180	800	successful
Southern white rhinoceros	248	31		24	230	successful
Black rhinoceros	19	0			21	successful
Hippopotamus	8	0			8	successful
Giraffe	77	0			85	successful
Greater kudu	160	10	release	240	c.800	successful
Eland	366	16	release	52	450	successful
African buffalo	19	0			31	successful
Common waterbuck	96	11	release		c.150	successful
Common reedbuck	108	0			c.100	successful
Sable antelope	67	1	accident		75	optimistic
Gemsbok	158	1	release	13	210	uncertain
Blue wildebeest	822	9	release	1361	400	successful
Cape hartebeest	902	7	release	517	600	successful
Tsessebe	70	1			75	successful
Impala	1937	16	release	1345	1000	successful
Springbok (a)	24	24	disease			failure
Springbok (b)	112	?	unknown		75	uncertain

Table 2. The species and numbers of animals that were released into the Pilanesberg National Park between November 1979 and August 1984, the number of deaths and removals between 1981 and August 1984, the status of each species in August 1984 and the considered result of each project.

second introduction, this time of animals from within the range of the disease, has not proved entirely successful since while no deaths due to Heart-water have been recorded the population has not increased (Table 2). Although the Springbok apparently occurred sporadically in Pilanesberg conditions may be suboptimal for year-round occupancy. The status of the population will be re-evaluated in October 1984 and if necessary the animals will be translocated to a more suitable area.

Condition on capture The capture and translocation of the Southern white rhinoceros *Ceratotherium s. simum* from the Umfolozi Game Reserve in South Africa took place when the population in that area was subject to severe nutritional stress because of below-average rainfall and overcrowding. The trauma of capture, combined with the subsequent 18-hour journey and sudden change in environment, had a particularly adverse effect on the animals, given their poor condition, and

resulted in a relatively high mortality rate (Table 2). Some rhinoceroses translocated during this period were so weak that they were unable to walk out of their crates or even to stand. Minimal losses occurred in rhinoceroses translocated during the late summer months when their condition was good. It should be noted that under normal circumstances animals in such poor condition would not have been captured; it was the severe drought then occurring in Umfolozi that compelled the removal of the animals since losses in the parent population may have been higher had the translocation not taken place.

Imbalanced sex ratios The methods involved in the large-scale capture of ungulates (Densham, 1974), which were used for some translocations to Pilanesberg, are selective against adult ♂♂ because breeding herds generally contain only one and because the close confinement of more than one adult ♂

during transportation usually results in fighting. In the year after the introduction of Blue wildebeest *Connochaetes taurinus* we found that only 4.3% of the population was made up of territorial bulls whereas in Umfolozi where the animals were caught they formed 14.5% (Attwell, unpubl.). Similar results have been obtained elsewhere for the Impala *Aepyceros melampus* (Brooks, 1975). Fortunately, for most species this kind of imbalance in the sex ratio of introduced animals does not persist after the subadult ♂♂ have reached maturity.

Capture techniques for the Southern white rhinoceros, on the other hand, tend to be selective against ♀♀ with small calves and towards adult ♂♂ (particularly territorial ♂♂). The consequence in Pilanesberg has been that the newly introduced population had a preponderance of adult ♂♂ in a ratio of 60:40. Furthermore, the age structure included no animals younger than one year and very few younger than three years. Thus the ♀ segment was comprised of mainly adult and subadult animals which meant that the population increased at a greater rate than that found in the parent population.

By virtue of their size Giraffes *Giraffa camelopardalis* are difficult to capture and transport as adults and consequently the introduced groups tended to consist of animals of a similar age. The actual transportation of the Giraffes to Pilanesberg posed no problems.

Disrupted social organisation The capture and translocation of animals interferes with the social organisation of most species in a number of ways. Capture during the autumn months, for example, disrupts the rut of most ungulate species in southern Africa which means that groups caught over this period are likely to have a lower conception rate than is normal for the year.

The introduction of African elephants into Pilanesberg was possible only if animals aged between three and five years were accepted. The family group which is so important in this species, where one dominant ♀ acts as leader, was thus broken; the leaderless calves showed atypical behaviour in that their daily

range was limited and the habitats they occupied were some of the most unfavourable of those available. The animals which died (Table 2) were the smaller ones of those introduced. To try to remedy the situation, a year after the 19 young elephants had been released two adult cows, which had been reared in captivity, were introduced into the area. These tame elephants provided leadership to a number of the calves and themselves reverted to wild behaviour. A subsequent release of elephant calves has resulted in the adult ♀♀ acting as leaders to a herd of 20.

Release methods Three methods of release were employed: (1) directly into the park (this was done for the majority of the animals), (2) into a large fenced holding area and (3) into a small, temporary enclosure. Care was needed in the siting of ramps used for off-loading animals; where one ramp faced a large dam six Common zebras *Equus burchelli* ran into the water and were drowned.

On release the animals did not always maintain the same social unit in which they were captured. The Southern white rhinoceroses, which were introduced over a period of 30 months, dispersed rapidly throughout the park from two release sites; there was some disruption of earlier established territories by ♂♂ which arrived towards the end of the exercise.

The translocation of a number of animals took place before the perimeter fence had been completed, so these were released into a 1200 ha fenced holding area. Unfortunately, the resources of this temporary enclosure proved to be inadequate for the number of animals held and 81 of them died, most as a direct result of the release strategy. Once the perimeter fence was complete the remaining animals were released into the park.

The release of Sable antelope *Hippotragus niger* involved the use of small temporary enclosures so as to allow the animals to regroup into their social units on leaving the transport vehicle; after a few hours in the enclosure the antelope were allowed to leave of their own accord through the opened gates. This method was partially successful in maintaining group cohesion on release.

Excessive numbers The species and total numbers removed between 1981 and August 1984 are listed in Table 2. When the stocking rate was refined the populations of Blue wildebeest, Cape hartebeest *Alcelaphus buselaphus caama* and Impala already introduced was found to have exceeded the recommended level. Since 1981, therefore, the numbers of these species have been controlled and reduced towards the recommended totals.

Since no wildlife census was taken prior to the reintroduction programme, it was later found that several of the species which already occurred in the park, the Greater kudu *Tragelaphus strepsiceros*, Mountain reedbuck *Redunca fulvorufa* and Warthog *Phacochoerus aethiopicus*, had obviously been present in greater numbers than anticipated. We have now revised the acceptable carrying capacity of each of these species upwards from Collinson & Goodman's (1982) recommended figures (Table 1) to: Greater kudu 750, Mountain reedbuck 1000 and Warthog 250, but most will require annual removals in order to maintain their numbers at these levels. Control of the species began in 1984. It is thought that the present size of the indigenous Bushbuck *T. scriptus* population (currently standing at c. 400) is probably also above the prescribed carrying capacity but numbers will not be controlled until results from monitoring the species and its habitat show this action to be justified.

The maximum recommended population size for the Southern white rhinoceros was revised upwards to 250 from 1982 but this proved to have been unwise since the area suffered severe droughts in 1983 and 1984. The population will now be maintained at 200 animals by the translocation of some excess animals to parks in other parts of the country and by the controlled safari hunting of adult ♂♂ in the hunting zone which makes up about 20% of the park.

OTHER CONSIDERATIONS

Genetic conservation Greig (1979) has argued that the genetic content of regularly interbreeding groups must be maintained when

wildlife introduction and reintroduction projects are conducted. The impact of this treatise has been such that some authorities and many conservationists have opposed the mixing of animals of the same subspecies which may occur as little as 100 km apart. The view adopted for the Pilanesberg project has been that prior to the artificial creation of subpopulations as a result of man's activities the opportunity for gene flow occurred throughout the range of a subspecies. One of the aims of the World Conservation Strategy is to maintain genetic diversity (IUCN, 1980), and little would be achieved towards this goal if introductions were confined only to one subpopulation of a subspecies. The fact that the elephant, Giraffe and zebra in Pilanesberg come from widely separated subpopulations is not, therefore, viewed with concern. Nevertheless, it is appreciated that some of the introduced populations will not be able to reach the level of genetic fitness which is considered adequate for long-term conservation (Soulé, 1980). Indeed some, like the Hippopotamus *Hippopotamus amphibius* and the elephant, must be regarded more as cosmetic populations than as ones which serve in the overall conservation of the species. It is accepted that with time the gene pool may have to be extended by further translocations.

Economic factors To justify the allocation of land for conservation in the face of the demand for livestock grazing it is becoming necessary in Third World countries for factors such as economic return and employment opportunities to be considered. With few exceptions the rate of increase of purchase prices of live game animals on the open market have exceeded bank interest rates and the rate of inflation in South Africa. Therefore, a number of Impala, Blue wildebeest and Cape hartebeest bought in 1980 were resold in 1981 at a profit. At present the revenue received from wildlife utilisation in Pilanesberg is approximately three times that obtained from tourism, but to achieve this return it has been necessary to build up the wildlife stocks as quickly as possible in a strategy that has also benefited

tourism. From the point of view of ecological balance it would, of course, have been preferable if smaller numbers of each species had been introduced and then allowed gradually to reach carrying capacity. In Pilanesberg however, sociopolitical factors called for the rapid establishment of the reserve and its wildlife populations.

CONCLUSIONS

In the restocking of an area with wildlife the carrying capacity, stocking rate, habitat suitability and endemic diseases present must be considered. An imbalance in the age/sex ratios as a consequence of the practicalities of capture and transportation techniques may temporarily affect the success of a project. When unloading animals from transport vehicles it is preferable to release them directly into a field or, should this not be possible, into a temporary fenced enclosure to allow them to re-establish their social groupings over a number of hours.

The Pilanesberg reintroduction project, where nearly 6000 animals of 20 species were relocated, is considered to have been highly successful and in 1984 an economic return of almost US\$250 000 was obtained from the sale of animals.

AUTHOR'S NOTE

All the animals released into Pilanesberg, with the exception of the elephants, have bred successfully since introduction. For most species it is impossible to determine the exact number of young produced (the Impala, for example, have given birth to over 1000 calves). We do know, however, that at least two Black rhinoceros calves have been born since August 1984, and that by 1985 the Hippopotamuses produced four calves, the Giraffes 33 and the buffalo 17. The Springbok population was re-evaluated in October 1984 and the numbers were found to have remained constant; it was decided, therefore, to translocate the animals to more suitable areas. In order that their immunity to Heart-water is not lost the areas to which the Springbok have been moved are ones in which the disease is endemic.

ACKNOWLEDGEMENTS

I would like to acknowledge the staff of the Pilanesberg National Park whose observations have contributed to this paper, in particular D. Parry, P. Hancock and R. Collinson. My thanks also to A. K. K. Hillman of the African Wildlife Foundation for information on the Black rhinoceros monitoring project.

REFERENCES

ACOCKS, J. P. H. (1975): Veld types of South Africa. *Mems bot. Surv. S. Afr.* No. 40: 1-128.

ANDERSON, J. L. (1984): A strategy for cheetah conservation in Africa. In *The extinction alternative*: 127-135. Mundy, P. J. (Ed.) Johannesburg: Endangered Wildlife Trust.

ATTWELL, C. A. M. (unpublished): *Reproduction and population ecology of the blue wildebeest Connochaetes taurinus taurinus in Zululand*. Unpublished Ph D thesis, University of Natal.

BROOKS, P. M. (1975): The sexual structure of an impala population and its relationship to an intensive game removal programme. *Lammergeyer* 22: 1-8.

COE, M. J., CUMMING, D. H. & PHILLIPSON, J. (1976): Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22: 341-354.

COLLINSON, R. F. H. & ANDERSON, J. L. (1984): Problems, principles and policy in the re-introduction of large mammals into conservation areas. *Acta zool. fenn.* 172: 169-170.

COLLINSON, R. F. H. & GOODMAN, P. S. (1982): An assessment of range condition and large herbivore carrying capacity of the Pilanesberg Game Reserve, with guidelines and recommendations for management. *Inkwe. Environmental Research in Bophutatswana* No. 1: 1-54.

DENSHAM, W. D. (1974): A method of capture and translocation of wild herbivores using opaque plastic material and a helicopter. *Lammergeyer* 21: 1-25.

FARRELL, B. & VAN RIET, W. (unpublished): *Pilanesberg National Park, Bophutatswana*: 1-79. Report to the Department of Agriculture, Bophutatswana.

GREIG, J. C. (1979): Principles of genetic conservation in relation to wildlife management in southern Africa. *S. Afr. J. Wildl. Res.* 9(3/4): 57-78.

IUCN (1980): *World conservation strategy*. Gland: International Union for the Conservation of Nature and Natural Resources.

RINEY, T. (1955): Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. *N. Z. Jl. Sci. Tech.* 36B: 429-463.

SOULÉ, M. E. (1980): Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation biology*: 151-169. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates.