

The relevance of life history theory to harvest and conservation

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Landa, A. 1997. The relevance of life history theory to harvest and conservation, - *Fauna norv. Ser. A.* 18: 43-55.

"Life history theory" and "applied ecology" are two disciplines that together span much of the field of natural science. The first seeks to understand the basic patterns underlying the diversity of life cycles, whereas the second seeks to guide our interactions with nature. In this paper I have concentrated on how life history theory relates to "harvest" and "conservation" of wildlife. Life history theory has the possibility to help make some general predictions about the interrelationship between demographic life history traits and interests of management and conservation. Theoretically it can therefore be used as a predictive tool which might allow us to extrapolate data from well-studied species to poorly-studied species with similar life history traits. However, life history theory has concentrated on broad patterns at scales that involve many different taxa, and has so far not always been successful in explaining the patterns that occur at finer taxonomic scales. Nevertheless, applied ecology would be a far more mature science if it had a greater contribution from life history theory. There are obviously a finite number of general patterns of life history variation which can be used to make general predictions. However, successful management will also need a better understanding of species in context of communities and ecosystems. We have to handle harvest and conservation on several levels of organisation simultaneously. Perhaps conducting in situ studies with a life history perspective will ultimately allow us to make more reliable predictions at a lower level of scale than is possible today. Furthermore, management actions could be treated as ecological experiments. This will not only help the managers understand the process of research, it will also provide many more tests of hypotheses with potential value for applied ecology.

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INTRODUCTION

No other living beings have a larger influence on nature than humans. The goal of applied ecology is to use the knowledge we have about ecological systems to guide our relationship with natural systems. Our relationship to nature consists of both exploiting and preserving natural resources. Our prime motivations are not scientific, however - they are either economic or ethical (Lawton 1997). Historically, the main uses of applied ecology were for harvesting biological resources and pest control programs; put simply, for species that we, as humans, either consider to be desirable or undesirable. Recently the discipline "conservation biology" has developed in parallel to the conservation portion of the discipline "wildlife management". The broad applied

ecological discipline of wildlife management covers the three related fields of harvest, pest control and conservation (i.e. Begon et al. 1990, Caughley & Sinclair 1994).

Almost all human actions will modify the size, structure and distribution of populations, and accordingly our management tools can operate on an individual level, and on a habitat level. In any management plan there are two important decisions that need to be made: 1) what is the desired goal, and 2) which methods do we use to reach this goal? In order to make these decisions wisely, we need biological information about the system in question. More specifically, we need to know how population size varies over time and space, and how our actions affect the system under study, at seve-

ral possible levels of organisation (individual, population community), at several spatial scales (local, regional) and at several temporal scales. Thus we need to be able to make predictions.

Applied ecology has remained a very much case by case science, some of which I will present later. Indeed, as pointed out by John Lawton (1997) "conservation action without good science to underpin it is like alchemy, or faith healing. Both sometimes produce desirable results, but you have no idea why, and mostly they do not." The problem that applied ecology is a science of application, which tends to lack underlying theory, is now widely recognised.

Life history traits, in the broadest sense, are all the ecological, behavioural, morphological and demographical characteristics, or traits, of a species (Stearns 1992). Life history theory seeks to understand the diversity of the life history traits that we see in nature. This is done by studying the correlations or trade-offs that exist between life history traits, in relation to ecological factors and phylogenetic constraints. Rather than being concerned with the short-term effects that humans have on nature, life history is built on studying the results of millions of years of evolution on traits that are geneti-

cally inherited and subject to selective forces. Thus the basic tenant of life history theory is natural selection. The principle life history traits that have received most attention relate to reproduction like age and size at maturity, number and size of offspring, age and size specific reproductive rates, and to survival, such as age and size specific mortality rates, and length of life. These are also the main parameters that are studied in applied ecology.

The discovery of many patterns of co-variation among traits, for example between relative age at first reproduction and relative life expectancy (i.e. Harvey & Zammuto 1985; Figure 1), based on empirical data have resulted in abundant theory. However, there have been relatively few attempts so far to apply this theory to real world conservation or harvest problems. For example, textbooks in the two disciplines, Stearns (1992), and Roff (1992) on life history and Caughley & Sinclair (1994), and Caughley & Gunn (1995) on applied ecology, contain only anecdotal notes about the other field.

There is clearly much potential for integration between these fields (Pimm 1991, Urban et al. 1992). The potential benefits of marrying the predictive power of life

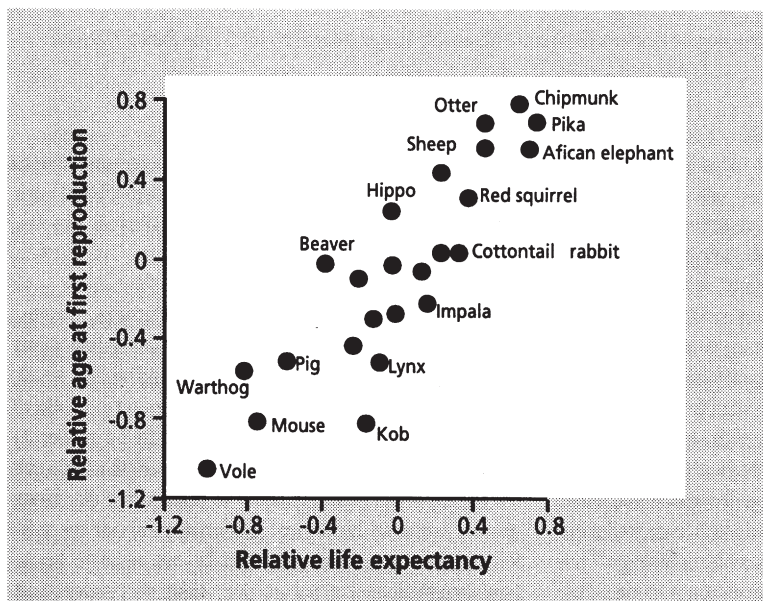


Figure 1
Relationship between relative age at first reproduction and relative life expectancy at birth for 24 species of mammals (after Harvey & Zammuto 1985).

history theory with the application of applied ecology are enormous. Yet, 1) how far have we come ?, 2) how could we use life history further in applied ecology? and 3) what would be the potential limitations of such a new, hybrid discipline of applied-life-history ? I will draw examples from two areas, harvest regulation and conservation biology.

Application of life history theory to the regulation of harvest

Harvest and population dynamics models

Human life is dependent on the harvest of natural resources. The most commonly stated goal of such harvest is to obtain as much as possible, but to do it in a sustainable way. Effective regulation of the harvest of a species is aided by having a detailed population model. The concept of maximum sustainable yield has traditionally been associated with the idea that a population should be maintained at a size where its growth rate is maximal (Caughley 1977). The first simple model of population dynamics that was used to describe population size with time was the logistic model, where the maximum population growth rate occurs when the population size is about half of its carrying capacity (see curve B, Figure 2).

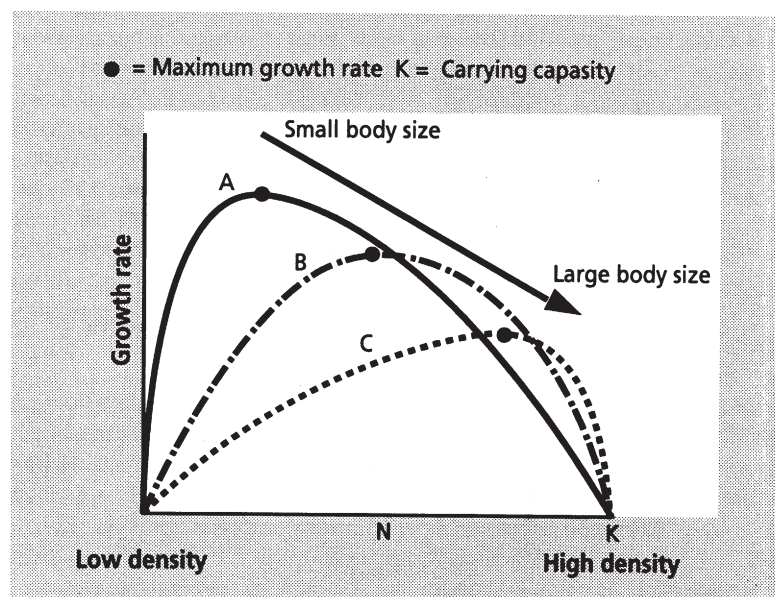
Fowler (1981) compared species' life history traits with empirical data on the nature of their response to density effects. He showed that the position of the maximum population growth rate, relative to the carrying capacity, was different for different species, depending on their body size and on their life history strategy. Species with high reproductive rates, short life spans and populations held below the limits of environmental resources exhibit most density-dependent change at low population levels (Figure 2, curve A). In contrast, species with low reproductive rates, long life spans and populations that are more limited by resources (large mammals in particular) show that most density-dependent changes in vital rates at levels of the population close to carrying capacity (Figure 2, curve C).

The aim of this kind of life history studies was not directed towards applied ecology. However, managers could have used this result to maintain different species at different relative densities to obtain the maximum productivity of the population in question.

Unfortunately, the logistic model is an oversimplification of the dynamics of any kind of population in a natural system, mainly because it ignores individual variation, sex and age structure of the population, and environmental stochasticity. Even if the managers had

Figure 2

Large mammals and similar species, (curve C), are expected to show most of their density-dependent change at population levels close to the carrying capacity (K). At the other extreme, many insects and other short-lived species are expected to show most density-dependence at lower population levels (curve A). B shows a symmetric productivity curve with maximum growth at 0.5 K (redrawn from Fowler 1981).



included life history theory into the determination of quotas, the shortcoming of this model would have led to management failures.

A fixed quota strategy has frequently been used to manage harvesting of populations. The dangers of fixed-quota MSY harvesting are well illustrated by whaling in the Antarctic during this century (Gulland 1971; Figure 3). Fixed quota Maximum Sustainable

Yield (MSY) led to the decimation of the whale populations in the southern oceans due to overharvest. The quotas set were believed to be sustainable. However, it is not recommendable to fix quotas at the MSY level itself, or to leave quotas unchanged from year to year (Begon et al. 1990). Figure 4 (after Caughley 1977), clearly illustrates what happens when the harvest is higher than the maximum sustainable yield. Increasing the harvest by 25 animals from 125 to 150 when 150 is

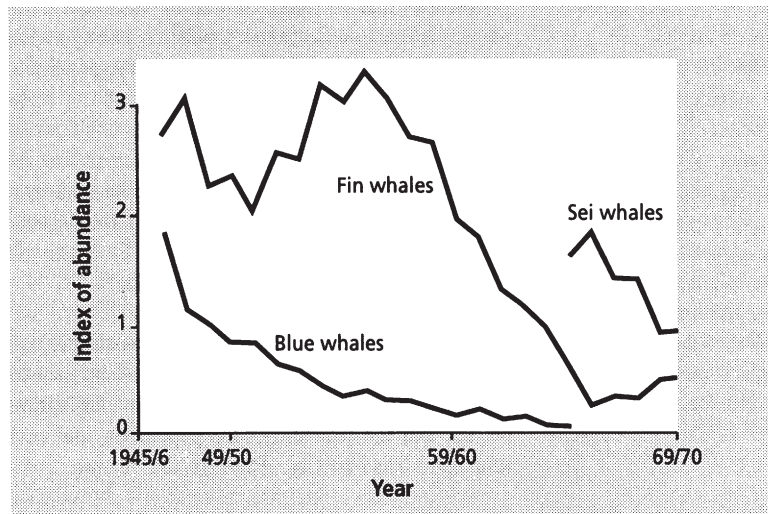


Figure 3

The declines in the abundance of Antarctic baleen whales under the influence of human harvesting (After Gulland 1971).

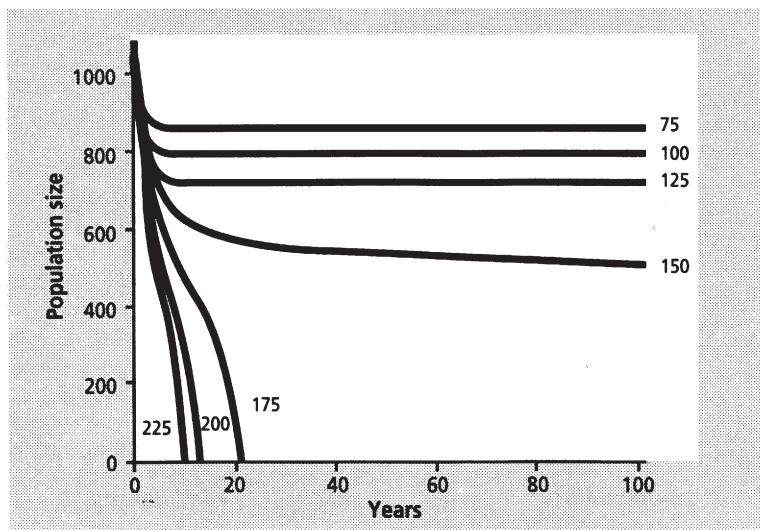


Figure 4

Trend in size of a population (logistic growth is assumed) when a constant number of animals is harvested each year. The maximum sustainable yield (MSY) is 150/year (after Caughley 1977).

the MSY, had relatively little effect, but the same increase from 150 to 175 would have a dramatic effect. Nevertheless, such harvest regimes require good population dynamics data and a close monitoring of recruitment and should not be based on waiting for low catches before changing the strategy.

So, we need to find and apply more realistic models for determining sustainable harvest. Models by Lande et al. (1995) and Sæther et al. (1996a) that are based on threshold-systems of harvest are one such development. Among their advantages are that they take into account the fluctuating and stochastic nature of real world population processes. They have concluded that the optimal strategies always included a threshold, with a maximum harvest rate above the threshold and no harvest below. The threshold is relatively independent of the form of density-dependence (Sæther et al. 1996a). The threshold decreases with decreasing environmental fluctuation and when the maximum rate of harvest decreases. A lower average harvest rate will lower the threshold and provide more years when harvest is possible. So far this work has only been theoretical and its applicability has not been tested in any management system. Nevertheless, like earlier works, they showed that the harvest strategy depends on the intrinsic rate of population increase, r , which is related to body size, and is a component of life history strategy (Figure 5).

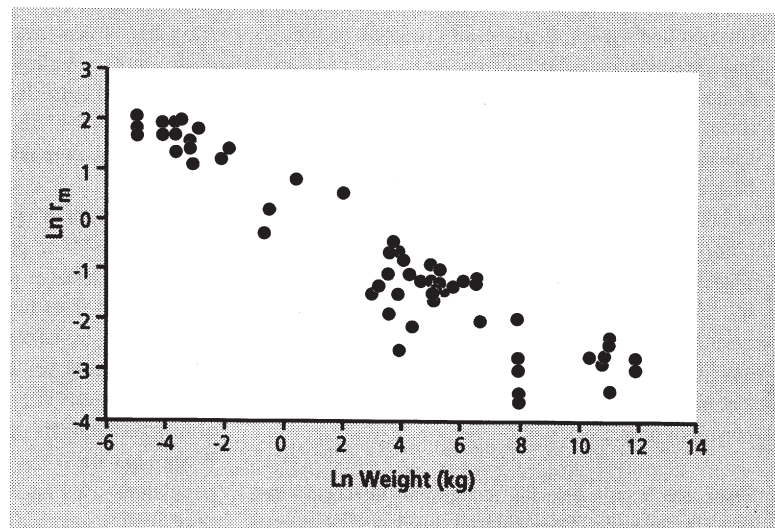
Harvest and implications of sex and age structure

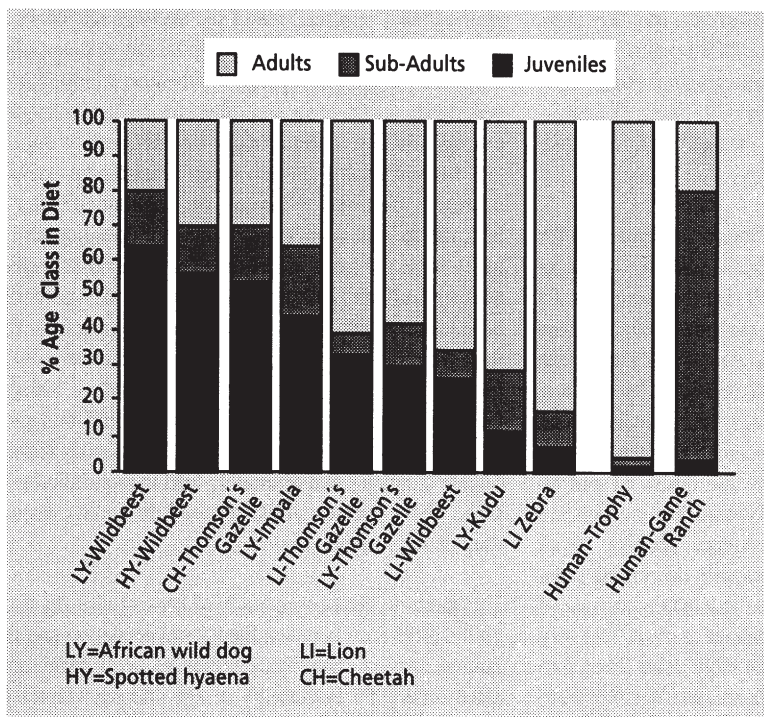
So far it appears that knowledge about demographic life history traits is an integral part of determining harvesting strategies. However, other life history traits, for example mating system, might be additionally important for sustainable harvest when determining harvest strategies. Sex-biased harvest on ungulate species is believed to have numerous effects, but does not necessarily have the same effect on all species. Ginsberg & Millner-Gulland (1994) investigated one such potential deleterious effect of sex-biased harvest caused by the males' limitations in their absolute ability to inseminate females. For example for impala (Ginsberg & Milner-Gulland 1994), sensitivity analysis showed that prolonged trophy hunting of males could seriously reduce female fecundity and ultimately lead to population collapse. Other species would respond differently depending on their mating system.

Furthermore, the consequence of harvest also depends on the difference between the natural predation and the human harvest. Hunting patterns of wild carnivores often reflect the availability of age and sex classes of the prey, whereas trophy hunters rarely kill ungulate age / sex classes in the same proportion as predators (Ginsberg & Milner-Gulland 1994). Hunters in Africa usually kill more adult males and fewer juveniles and females than lions, hyaenas and hunting dogs (Figure 6). Therefore, human harvest interferes with natural

Figure 5

Natural log of the intrinsic rate of increase (r_m) as a function of natural log body weight of 61 different species (after Sinclair 1997).



**Figure 6**

Selection of ungulate prey, by age class, by different natural predators in Africa. Most predators preferentially kill juveniles, but there is no exclusive predation on a single age class for any prey species. By contrast, humans show strong preference for either adults (trophy hunting) or yearlings (game ranching). Figure after Ginsberg & Milner-Gulland 1994, see original paper for data sources.

predation - prey processes. A successful management strategy requires information both on general biology of the species and its interrelationship with other species.

Harvest and the implications of evolution of life history traits

Although we are only just beginning to understand the consequences of changing the way selective forces operate on life history traits, there is cause for concern. Indeed, by modifying life history traits through selective hunting, we may modify the productivity of populations, which in turn could affect our harvest strategies. Therefore, we need to consider the impacts of human selective harvest. We are reminded of the power of artificial selection every time we see a poodle or a dachshund on the street. It was not long ago that their ancestors were wolves, running through the boreal forest in pursuit of prey.

There has been a growing recognition in recent years that size-selective harvesting produces selection pres-

sure within the exploited population. This could induce evolutionary shifts in such characters as age at maturity, growth rate, and the timing and magnitude of fecundity. For example most fisheries employ a minimum mesh size of nets to selectively catch the largest individuals. Such selection for large individuals has been hypothesised to explain low body weight and early age at maturity in the North Sea cod (Rowell 1992), as well as in Norwegian reindeer (Skogland 1989).

Indeed, changes in age and size specific mortality rates caused by a shift in predation pressure can cause rapid evolutionary change in life history traits in the predicted direction. This has been demonstrated by Reznick et al. (1990), based on long-running experiments manipulating stage-specific mortality, due to predators, in field populations of guppies. Thus, harvesting not only affects the numbers of individuals within a population, it can also affect the age, size, and sex structure of a population. This implies that harvest is operating as a selective force on life history traits. A major problem is

that this selection may be operating in ways very different from those under which the species has evolved.

Because harvest influences life history, the concept of Evolutionary Stable Optimal Harvesting strategies (ESOHS) has been proposed. Law & Grey (1988, 1989) raised the question of whether such harvesting strategies are possible. An ESOHS would be one that: 1) Over long periods of time, imposes no selection pressure on individuals in the exploited population to change the life-history characteristics expressed in future generations, other than the original, natural selection pressure and 2) The harvester cannot increase the sustainable yield by changing the strategy. Blythe & Stokes (1991) showed how simple stage- and size structured models may be used to assess the possible evolutionary consequences of size-selective harvesting regimes. In another paper (Stokes & Blythe 1991), they used this model to qualitatively assess possible changes in the exploited populations that might result from management actions, such as altering mesh size and hence size at capture and/or harvesting rate.

There will always be dangers in basing harvest models on predictions, or extrapolated data. This will be especially important for intensively harvested species, where errors in parameter estimation may have large consequences. Another problem arises from intraspecific variation in life history parameters. For example, Norway is a long and diverse country, with many different ecological conditions. These ecological differences are reflected in the different reproductive strategies of moose in Northern Norway, compared to those in the south. Northern moose grow faster and mature later than moose in the south (Sæther et al. 1996c). Another example is provided by Scandinavian brown bears. They also grow faster and mature later in the north, but also have far higher rates of population increase (Swenson et al. 1997, Sæther et al. 1997) than would have been predicted from North American studies (Craighead et al. 1974, Wielgus & Bunnell 1993, Wielgus et al. 1994).

This clearly shows that life history theory needs to be able to explain both intra- and inter-specific patterns of variation in life history traits before its full potential as a predictive tool can be realised.

Application of life history theory to conservation biology

Individual life histories are at the heart of conservation biology because, to quote Dean Urban et al. (1992), "biodiversity can be explained in terms of an interplay between life history mechanisms and environmental constraints". In other words, the forces of evolution, like climate, resource availability and disturbances, have acted on demographic processes of growth, recruitment and mortality to produce the biodiversity that conservation biology is trying to protect (Figure 7).

There is no doubt that biodiversity is in need of protection in our rapidly changing world. Given the impossibility of studying all of the millions of species that exist worldwide in individual detail, a tool that could predict a taxon's persistence, resilience, abundance and response to environmental change would have many applications. The main question is how. And what role will life history theory have in this process?

Conservation biology consists of assessing risks (studying species decline and the causes of this decline) and of evaluating possible management plans. Risk assessment studies have shown that most species declines are related to small population size and habitat changes. Caughley (1994) emphasised that theoretical knowledge of small population dynamics was impor-

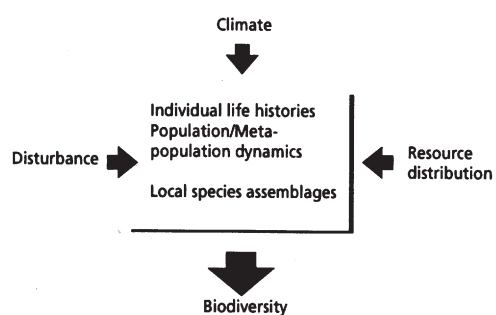


Figure 7

The forces of evolution, like climate, resource availability and disturbances, have acted on demographic processes of growth, recruitment and mortality to produce the biodiversity that conservation biology is trying to protect (Redrawn from Urban et al. 1992).

tant for risk assessment. The difference in abundance of populations of different species is a classical problem where life history has been included in an ecological context.

One of the classic ecological patterns provided by life history theory is Damuth's holes (Damuth 1987). In a simple log plot of species abundance against body weight, Damuth (1987) found that there are no species that are both large and abundant, or small and rare (Figure 8). As abundance is one of the factors determi-

ning risk of extinction, such patterns help by predicting that large species may therefore be at greater risk than smaller species. However, questions have been raised about the existence of this pattern at finer taxonomic scales, and there is a risk of making generalisations and oversimplifying the problems. Life history has also been shown to affect species resilience to chance events. Following a hard winter in England, bird species with higher egg production size returned to their former level of abundance faster than species with smaller egg production (Pimm 1991; Figure 9).

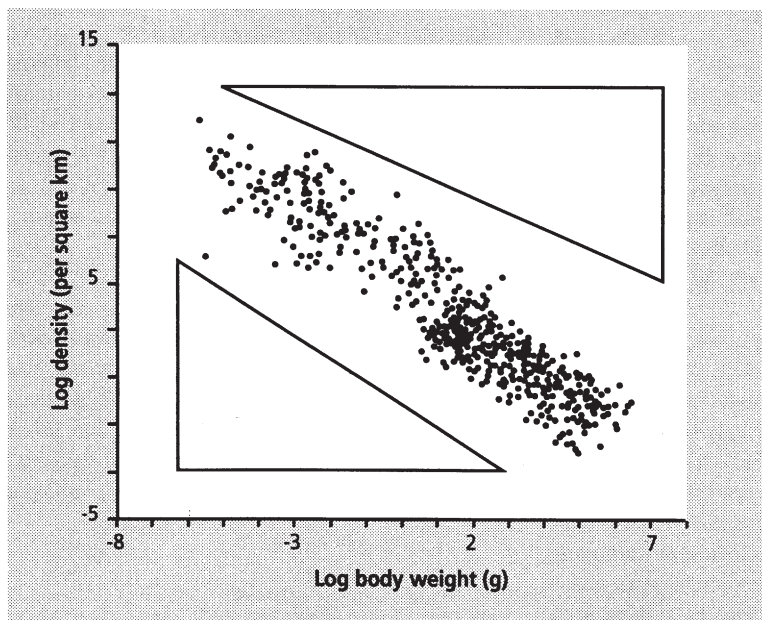


Figure 8

Species are either small and common or large and rare. No species occur within the triangular areas which are called Damuth's holes (After Damuth 1987).

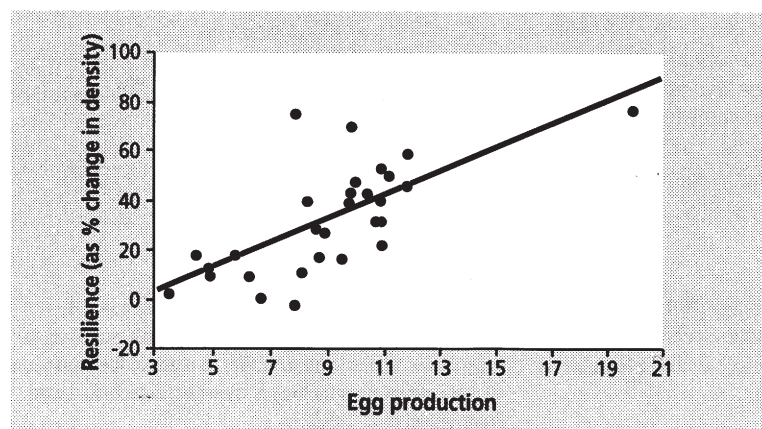


Figure 9

Bird species with a larger egg production have a greater resilience (example from resident British birds, after Pimm 1991, see original literature for further details).

In studies of the relationship between the developmental patterns of bird species and the key factors affecting their population dynamics, Sæther and co-workers (1996b) found that species with precocial young were most affected by events during the breeding season. Species with altricial young were most affected by events during the nonbreeding season. Therefore, if a perturbation occurs in a given season, the different species will respond differently depending on their life history strategies. Thus, in a given environment, different species may experience the same negative environmental effects, but the degree to which they are buffered from these effects will depend on their life history strategies. This implies that species are not simply passive responders to a stochastic environment.

These few examples clearly show that patterns exist between common life history strategies (like body weight, litter size and birth weight) and parameters that determine the sensitivity to environmental change and the risk of extinction. So far, then, it appears that general patterns can correlate life history and risk. But can we use this knowledge in practice?

The previously mentioned bird example suggested that large clutches correlated with high resilience (Pimm 1991). However, arctic foxes, a species with large litters, continue to decline in Scandinavia despite nearly 70 years of protection, whereas the wolverine (a species with smaller litter size) began to recover shortly after being protected from hunting. Both species were previously over-hunted in south Norway during the early decades of this century (Landa 1997, Landa & Skogland 1995, Landa et al. in press). These carnivore species showed patterns opposite of the predicted patterns from the bird study. Despite differing in body size (arctic foxes 3-4 kg, wolverines 8-18 kg) the species share many of the same food habits (Myhre & Myrberget 1975; Magoun 1987; Garrott & Eberhardt 1987; Landa et al. 1997, Landa et al. in press). However, they differ in a number of other aspects, e.g. wolverines utilise a much broader niche (both alpine, sub-alpine and woodland zones), whereas arctic foxes confine their activity to a narrow range of alpine habitats (Landa et al. in press), probably because arctic foxes are more constrained by inter-specific interactions at lower altitudes (Hersteinsson & Macdonald 1992). Although arctic foxes use only a narrow range of habitats, their

relatively small home ranges implies that a relatively large population of arctic foxes could occupy an area that might contain only a few wolverines. Within many of the alpine areas in Scandinavia, there is theoretically room for many more arctic foxes than the number found today. Thus, it is not a lack of space or dens that explains the present low numbers of arctic foxes in Scandinavia. Further research on arctic foxes must concentrate on identifying the failure of the population to recover during 67 years of protection despite the apparent presence of suitable habitat and breeding potential of arctic foxes (Hersteinsson et al. 1989, Landa 1997, Landa et al. in press).

As I have shown for both harvest and conservation, broad life history patterns may help us determine: 1) which types of species are at greater extinction risks and 2) how harvest strategies may account for complex life history strategies and the sensitivity of life history traits to environmental changes. However this has to be combined with more detailed knowledge to undertake any kind of management or conservation actions at a local level. Indeed, other key points are: 1) solving methodological problems, like estimates of populations sizes or estimating demographic patterns, 2) evaluating whether species are rare or abundant and 3) giving ourselves the tools and economics to realise conservation duties (i. e. Clark et al 1996; figure 10).

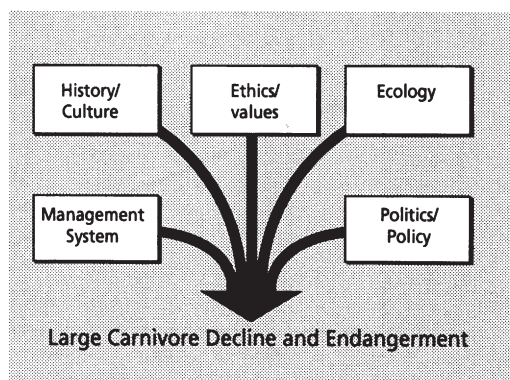


Figure 10

Most conservation issues involve multi-problem solving, with the ecological aspect being only a minor part of whole complex, here illustrated by a schematic representation of the five-part problem definition for large carnivore conservation in North America (redrawn from Clark et al. 1996).

Furthermore successfully conserving populations, species, or biological diversity, also involves a full understanding of ecosystem dynamics and the role of species in a community context. This can be illustrated by an example from a carnivore community. Indeed, no species lives alone on a flat white plain. They are organised into communities within ecosystems. Among carnivores complex systems of interactions, such as, intra-guild competition might exist. The result of this competition can be seen in the relative densities of cheetahs (Caro 1994) and African hunting dogs (Creel & Creel 1996) in various protected areas in Africa. Where lions and hyaenas are abundant, cheetahs and hunting dogs are rare. (Caro 1994, Creel & Creel 1996). The underlying mechanisms appear to be intra-guild predation on neonates for cheetahs, and kleptoparasitism for hunting dogs (Figure 11).

This means that we have to handle harvest and conservation on several levels of organisation simultaneously. To understand our impact on any single species, we must understand the mechanisms of interaction among them.

CONCLUSIONS AND QUESTIONS

As these examples have shown, life history theory has the possibility to help make some general predictions about the interrelationships between demographic life history traits and parameters of management and conservation interest.

Indeed, making an accurate population model for a given species requires detailed knowledge of demographic characters, data which are lacking for most populations that are presently being harvested worldwide. There is therefore a clear need for predictive tools that might allow us to extrapolate data from well studied species to poorly studied species with similar life history traits.

I have also pointed out some of the practical and theoretical problems that may occur. It seems that whereas life history theory has concentrated on broad patterns at scales that involve many different taxa, it has so far not always been successful at explaining the patterns that occur at finer taxonomic scales.

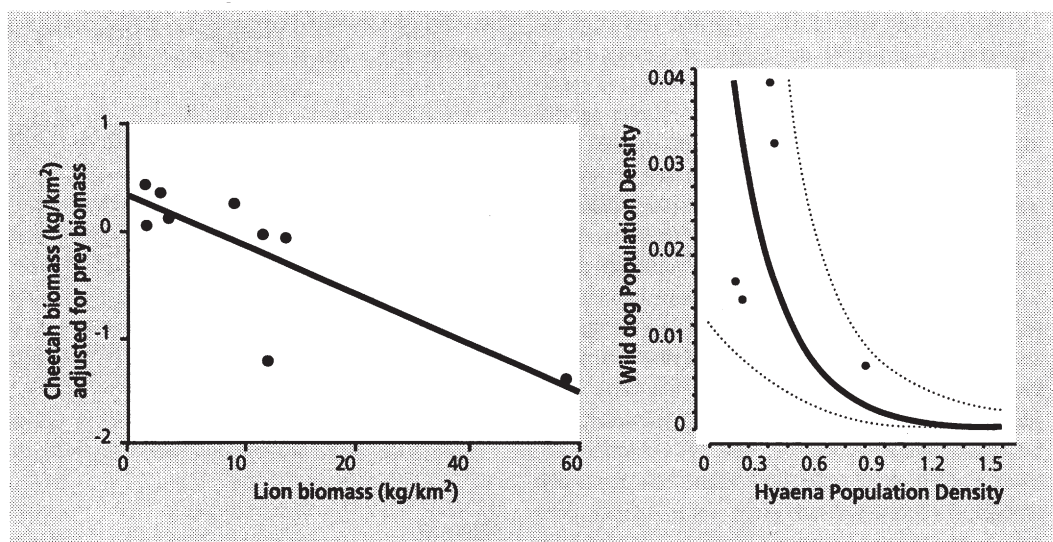


Figure 11

The density of cheetahs and African wild dogs is best explained by the density of larger predators (lions and hyaenas). The underlying mechanisms appear to be intra-guild predation on neonates for cheetahs, and kleptoparasitism for hunting dogs (cheetah: after Caro 1994, wild dog: after Creel & Creel 1996).

This does not mean that life history theory cannot offer helpful insights at these fine scales, it is just that greater resolution will require that more traits will be needed in the analysis. Information on dispersal, niche width and response to environmental variation may be required, for example.

However, the more data that is needed, the less practical the tool will be for making predictions

My conclusion can only echo that of John Lawton (1992) when discussing whether 10 million species had 10 million different population dynamics. Yes, - and no. There are a finite number of general patterns of life history variation. These can be used to make general predictions. Applied ecology would be a far more mature science if it had a greater contribution from life history theory. However, at the present, if we want to predict the life history strategy, ecology and population dynamics of a certain species in a certain habitat in detail, there is no alternative but to study that species in situ. Perhaps conducting such studies with a life history perspective will ultimately allow us to make more reliable predictions at a lower level of scale than is possible today.

Even if we as biologists (both those that study life history theory and applied ecology) can work together to model and understand nature and the effects that we have on it, there is still one problem. How do we translate our knowledge into better management? We need to be better at explaining our knowledge to managers.

We have generally failed to use management actions as ecological experiments. Perhaps one way of developing better biologist - manager relationships is to treat more management actions as experiments. There are many authors, which have called for this (i.e. Romesburg 1981, Macnab 1983, Fraser 1985, Gavin 1991, Murphy & Noon 1991, Nudds & Morrison 1991, Peterson 1991, Nichols 1991, Sinclair 1991, 1996). This will not only help the managers understand the process of research, it will also provide many more tests of hypotheses with potential value for applied ecology.

ACKNOWLEDGEMENTS

This paper originally resulted as a given theme for the fulfilment of my PhD study at Norwegian University of Science and Technology (NTNU), Trondheim, with the original title "The relevance of life history theory to applied ecology". I thank John Linnell, Anne Loison, Jon Swenson, Olav Strand, Erling Solberg, Eivind Røskoft and Bernt Erik Sæther for valuable comments on earlier drafts of this paper. I especially acknowledge the guidance and help to clarify and structure this paper given by Anne Loison and John Linnell.

SAMMENDRAG

Betydning av livshistorie - teori for høsting og bevaringsforvaltning

"Livshistorie teori" og "anvendt økologi" er to disipliner som omfatter store deler av biologisk forskning. Den første søker å forstå de grunnleggende mønstre bak livssyklus, mens den andre prøver å gi et grunnlag for våre interaksjoner med naturen. Jeg har konsentrert meg om hvordan livshistorie-teori henger sammen med disiplinene høstings- og bevaringsbiologi. Dette er de to områdene som har størst anvendelighet for Skandinavia i dag. Det synes som om livshistorie teori har konsentrert seg om "grove mønstre" på målestokker som involverer mange forskjellige taksa, men har så langt ikke alltid kunne forklare mønstre som finnes når en studerer arter på finere målestokker. En vellykket bevaring av populasjoner, arter, eller biologisk mangfold, er ikke bare en økt kunnskap om arters livshistorie strategier, men involverer også en full forståelse av dynamikken i økosystemer. Med andre ord vi må forstå artene i kontekst av samfunn og økosystem. Dette betyr at vi må behandle høsting og bevaring på flere organisasjonsnivå samtidig. Vi mangler slik detaljert kunnskap for de fleste populasjoner som i dag høstes verden over. Det er derfor et klart behov for et verktøy som kan forutsi effektene av våre handlinger og dermed tillate oss å overføre kunnskap fra godt studerte arter til mindre studerte arter med liknende livshistorie trekk. Livshistorie-teori kan hjelpe oss i å gi generelle prediksjoner om sammenhenger mellom demografiske livshistorie trekk og forvaltning. Anvendt økologi ville ha vært en langt mer "moden" vitenskap med et større

bidrag fra livshistorie teori. Det finnes et uendelig antall av generelle mønstre av livshistorie variasjon som kan benyttes for å gi generelle prediksjoner. Likevel, dersom vi ønsker å prediktere livshistorie strategi, økologi og populasjons dynamikk i et spesielt habitat og for en bestemt art, i detalj, så finnes ikke noe annet alternativ enn å studere vedkommende art i det aktuelle habitatet. Dersom slike studier ble utført innenfor et livshistorie perspektiv ville vi kanskje kunne tillate oss å gi mer pålitelige prediksjoner på et "finere" nivå enn hva som er mulig i dag. Fra et forskningssynspunkt burde flere forvaltnings handlinger vært utført som økologiske eksperiment. Dette ville ikke bare øke forvalterenes forståelse for forskningsprosessen, men ville i tillegg gi mange flere tester av hypoteser med potensiell verdi for anvendt økologi.

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APPENDIX

Latin names for species in text:

Arctic fox, *Alopex lagopus*
 Brown bear, *Ursus arctos*
 Cheetah, *Acinonyx jubatus*
 Domestic dog, *Canis familiaris*
 Guppies, *Poecilia reticulata*
 Hunting dog, *Lycaon pictus*
 Hyena, *Crocuta crocuta*
 Impala, *Aepyceros melampus*
 Lion, *Panthera leo*
 Moose, *Alces alces*
 North Sea cod, *Gadus morhua*
 Reindeer, *Rangifer tarandus*
 Wolf, *Canis lupus*
 Wolverine, *Gulo gulo*