The Limits to Exploitation on Land and Sea [and Discussion]

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The limits to exploitation on land and sea

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SUMMARY

The sustainable yield of a population can be related directly to its demographic parameters and density-dependent processes. For fish stocks a direct and simple relationship can be derived relating this yield to the level of natural mortality and the stock and recruitment relationship. For terrestrial mammals, a plethora of different density-dependent processes have been identified. A derivation of a stock and recruitment relationship for terrestrial mammals is described here and applied to data on certain mammals. The comparative response to harvesting of marine species with these terrestrial mammals is then examined.

1. INTRODUCTION

The ability of a population to produce a sustainable yield under harvesting pressure depends upon its density-dependent responses to resource limitation. This somewhat superficial generalization is the basis for the comparison in this paper of the mechanisms of density-dependent responses in marine and terrestrial populations and their ability to sustain yield.

Although density dependence is the key to sustainability, the underlying demography of populations is critical in determining the level of yield. This is the essence of the simplest population models which relate the yield to the intrinsic rate of increase. In the marine system, Gulland (1971) focused the problem by considering yield as a proportion of the unexploited biomass and went on to argue that this proportion was related only to the natural mortality rate of the species.

In this paper, following Gulland, we first pose the simple question: what determines yield as a proportion of the unexploited stock? We then consider the obvious generalization of this idea which allows for environmental variability and finally ask: how resilient are populations to overexploitation?

The paper concentrates primarily on vertebrates and, in the case of terrestrial systems, mammalian vertebrates. There are two reasons for this. The first is that species of interest for exploitation in terrestrial systems are usually vertebrate (arthropods and other insects are more usually part of pest control programmes). The second is that data that can be used for the purposes outlined are limited: few organisms have been studied sufficiently, so that their response to exploitation can be fully assessed.

2. MARINE POPULATIONS

In marine systems it has been conventional to consider that the density-dependent response occurs in the stock and recruitment relationship. This generalization is almost certainly invalid, but it seems clear that the density-dependent response of recruitment dominates the processes which affect the ability of species to sustain harvesting. The very high productivity of fish species in terms of egg production means that between egg and mature fish there is a massive level of mortality which, in principle, can occur at any of the stages of egg, larvae and young fish; see Rothschild (1990) for a review of this problem.

Various hypotheses about the mechanisms that determine the relationship between stock and recruitment have been posed eg Ricker (1954), Beverton & Holt (1957) and Cushing (1973) and deterministic forms to describe the stock and recruitment relationship abound. However, most types can be described relatively simply using a form suggested by Shepherd (1982*b*). These forms are illustrated in figure 1.

The relationship between stock and recruitment and the parameters of growth and mortality can be used to assess the response of a population to exploitation and to answer the question posed in this paper. Gulland (1971) had proposed that the equation

$$Y = \tfrac{1}{2} M B_0 \qquad (1)$$

provided a good approximation to the maximum sustainable yield Y of a population. M is the natural mortality rate and B_0 the unexploited population biomass.

Shepherd (1982*a*), using simple production models and Beddington & Cooke (1983), using a full age structured model had indicated that for most areas of feasible parameter space equation (1) overestimated yield.

Recently, Kirkwood *et al.* (1993) have investigated these problems and derived simple relationships between yield (and its variance) and the parameters of mortality and growth and the degree of density-dependent response as encapsulated by the stock recruitment relationship.

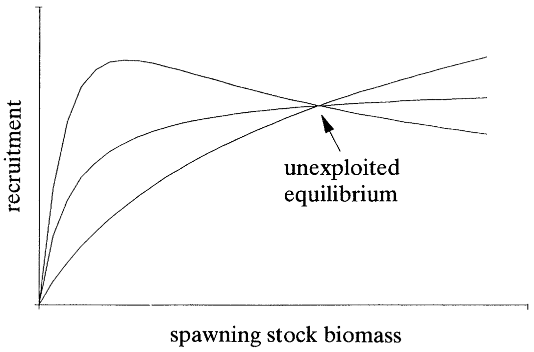


Figure 1. Various types of stock and recruitment relationships showing different degrees of density dependence.

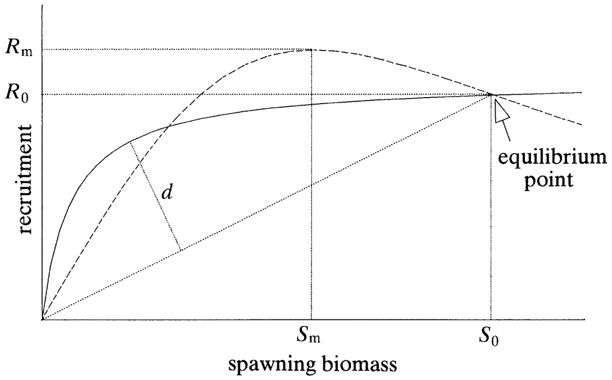


Figure 2. Different stock and recruitment functions described by Shepherd (1982*b*). 'Ricker type' can be described by the parameter R_m/R_0 and 'Beverton & Holt type' by the parameter d. Solid line, $d = 0.6$; dashed line, $R_m/R_0 = 1.2$, $S_m/S_0 = 0.6$.

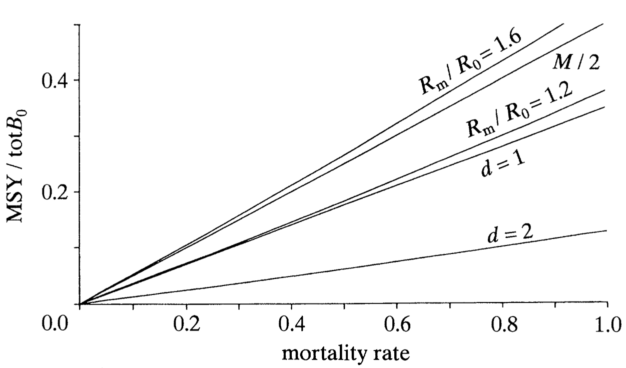


Figure 3. Yield as a function of natural mortality rate for different levels of density dependence in the stock and recruitment relationship. The line yield equals $M/2$ is drawn for comparison.

Kirkwood *et al.*'s analysis used the standard formalism for the dynamics of the population of Beverton & Holt (1957) and need not be described here. The derivation of their results depends on a parameterization of density dependence illustrated in figure 2 which indicates how the degree to which recruitment holds (or increases) with decreasing stock size can be simply described by a single parameter. The results on the level of yield as a function of mortality and this parameter are illustrated in figure 3.

In essence, there is a relationship between the yield and natural mortality which is approximately linear for all forms of stock and recruitment relationships. Unsurprisingly, the more extreme the density-dependent response, the higher the sustainable yield. Surprisingly, the relationship appears to hold over a very large range of values with natural mortality corresponding to life spans of less that one year through to life spans of tens of decades. This generalization appears to be robust and the question is whether a similar generalization can apply to terrestrial systems, where the density-dependent processes are so different?

3. TERRESTRIAL

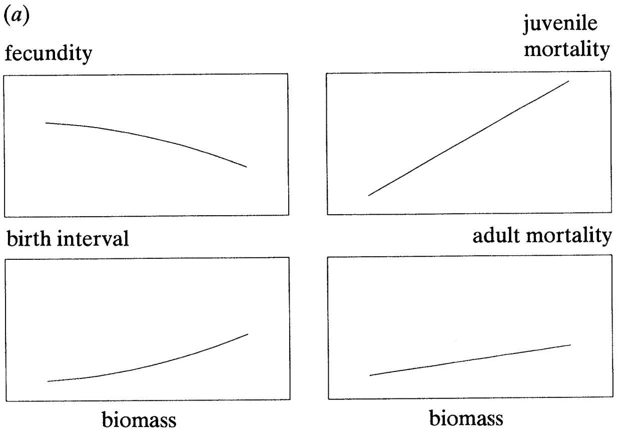
Inspection of the literature on population dynamics of terrestrial mammals reveals a wealth of variation in the demographic response to changes in density and environment. The parameters that are observed to change are necessarily linked to the broad processes of demography and relate to birth rates and death rates, but within this constraint authors have amassed a vast number of parameters which relate more or less loosely to these key variables. It is thus somewhat daunting to consider whether it is possible to derive some form of generalization about the response of terrestrial mammals to exploitation.

We have sought this generalization in a derivation of the relationship between stock and recruitment for terrestrial mammals. The attractions of such a generalization are obvious as, if it proves possible, the results of the analysis of marine populations become applicable and, hence, some degree of synthesis is possible.

The stock and recruitment relationship for marine species is relatively simple in concept, but it depends on an important implicit assumption that the age of recruitment is that beyond which no further density-dependent processes occur. In terrestrial mammals this is somewhat more complicated as density dependence operates at larger ages. However, in practice, we have found that the existence of density dependence at high ages does not seriously alter the basic derivation of the stock and recruitment relationship, nor bias significantly the estimates of sustainable yield. However, it is clearly sensible to utilize an appropriate age at recruitment where at least the main effects of density-dependent mortality in young have ceased, and this has been done.

In principle, it should be possible, given reasonable monitoring, to derive from direct observation a stock and recruitment relationship for mammals; the observations required being simply those of the abundance of the sexually mature stock, some idea of its biomass and observations on the subsequent progeny. Such observations may well exist, but we have found only one case where that is sufficiently documented to enable a direct estimate to be made.

Instead we have adopted the procedure of fitting various density-dependent relationships for different demographic parameters, using them to define the necessary components of a population model and then manipulating that population model to deduce from it the way in which recruitment varies with stock. This process has been examined using appropriate simulation techniques to see that it does indeed reflect both



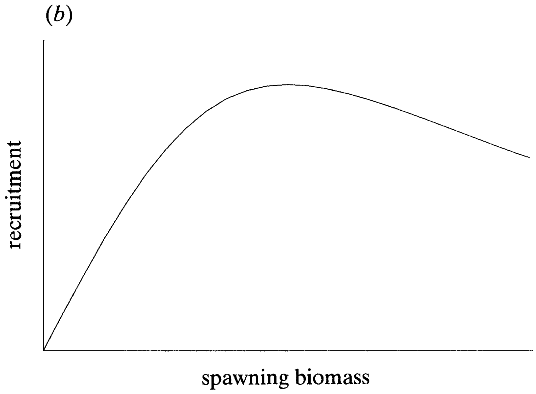


Figure 4. Schematic illustration of density dependence in demographic rates (*a*) leading to a derivation of a stock and recruitment relationship (*b*).

the true form of the stock recruitment relationship and the underlying dynamics of the stock. There are obvious complications and distortions as the age structure can be manipulated in a number of ways to produce, for the same stock size measured as biomass, different levels of recruitment. However, for the purposes of deriving a simple deterministic stock and recruitment relationship, the appropriate stationary age structure has been preserved.

Figure 4*a* illustrates the basic principle of the derivation. Density-dependent relationships in fecundity and mortality are used to derive an appropriate population model. This is then manipulated to assess for different parent stock sizes the production of young. The stock recruitment relationship so derived is illustrated in figure 4*b*. Clearly, the degree of plasticity in the density-dependent response will influence the shape of the stock recruitment relationship. In this paper we have not sought to generalize about these relationships, but have concentrated on some examples. Possible generalizations will be considered elsewhere.

(*a*) *Mammal case studies*

Despite the significant level of research that has been undertaken on terrestrial mammals over the past three decades, there is surprisingly little information which is complete enough to enable full population models of the dynamics to be developed. Of those available we considered in detail only a few species which have life spans in the range of some 10–50 years. It thus must remain an open question as to whether shorter-lived terrestrial mammals have similar demographic processes and can thus form part of the synthesis. In the case studies detailed below, the main problems and principles are illustrated.

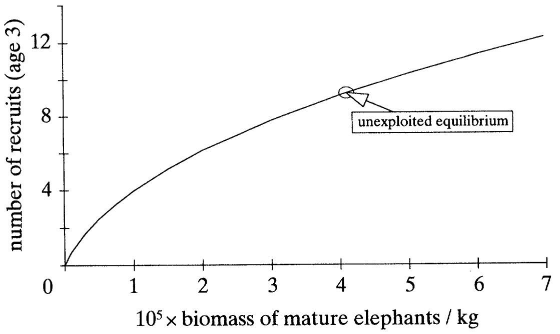


Figure 5. Stock and recruitment relationship derived for elephants (per 100 km^2).

(*b*) *Elephants*

The population model developed for elephants was based on a population similar to that of the Murchison Falls National Park (South). Basic schedules of age specific mortality were derived from Laws & Parker (1968). Density dependence of juvenile mortality, interbirth period and age at first breeding were derived from Fowler & Smith (1973). A Von Bertalanffy growth curve was derived from data in Hanks (1979).

The stock and recruitment relationship derived from these relationships is illustrated in figure 5. The relationship, unsurprisingly, shows relatively weak density dependence with recruitment declining monotonically with adult stock. In the parameterization of figure 2, the relationship would be seen to be of a Beverton & Holt type with a parameter of $d \simeq 0.2$.

The yield, as a proportion of unexploited biomass, is somewhat lower than 1% which is plausible. More unexpected is the result that the stock level at which the maximum yield can be taken is around 37% of the unexploited level.

(*c*) *Red Deer*

The population modelled was that inhabiting the Isle of Rhum, the detailed model was derived for the 'North Block'. Mortality schedules were derived from Beddington (1973) and Clutton-Brock & Albon (1989). Density dependence in juvenile mortality was fitted to data in Clutton-Brock & Albon (1989). In the case of fecundity, following the method of Beddington (1973) a distinction was made between yeld hinds (females which did not produce a calf in the previous year) and milk hinds (females which had produced a calf in the previous year). The fecundity of yeld hinds showed no trend with density, the fecundity of milk hinds was modelled using data in Clutton-Brock & Albon (1989).

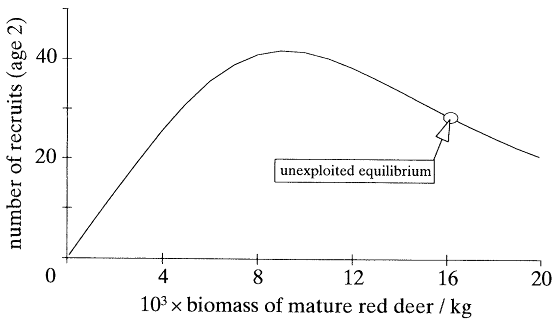


Figure 6. Stock and recruitment relationship derived for red deer, North Block, Rhum.

The stock and recruitment relationship derived from this exercise is illustrated in figure 6. It shows a marked increase in recruitment as adult stock is reduced below the unexploited level, the parameter R_m/R_0 is around 1.4. The maximum yield is estimated as being just under 15% of the unexploited biomass, and is taken at a biomass level of around 56% of the unexploited level.

(*d*) *Reindeer*

The population modelled is that of Hardangervidda in Norway. The schedules of mortality were derived from Skogland (1990), Reimers *et al.* (1983) and Helle & Kojola (1993). Density dependence in juvenile mortality was derived from Skogland (1990) and in fecundity from Skogland (1985). A Von Bertalanffy growth curve was fitted to data in Reimers *et al.* (1983).

The stock and recruitment relationship derived from these relationships is illustrated in figure 7. The relationship indicates a modest increase in recruitment as the adult stock is reduced below the unexploited level. In the parameterization of figure 2 the parameter R_m/R_0 is around 1.05. The maximum yield is estimated as around 8% of unexploited biomass and this yield is taken at a level of around 40% of the unexploited level.

4. MARINE AND TERRESTRIAL COMPARISON

The three case studies set out above indicate that there does appear to be a well-defined relationship between stock and recruitment which is similar to that which has been observed for fish species. This implies that it is possible to derive estimates of the response of these species to exploitation in an analogous manner to marine species.

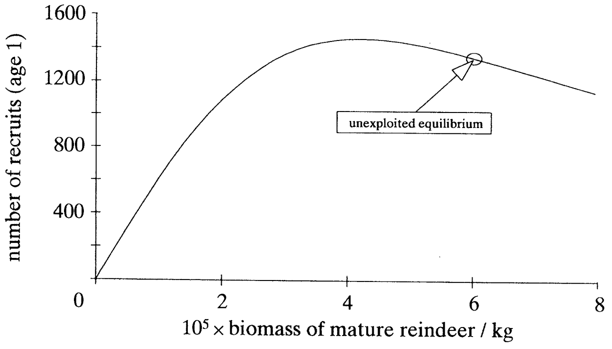


Figure 7. Stock and recruitment relationship derived for reindeer, Hardangervidda (per 8000 km^2).

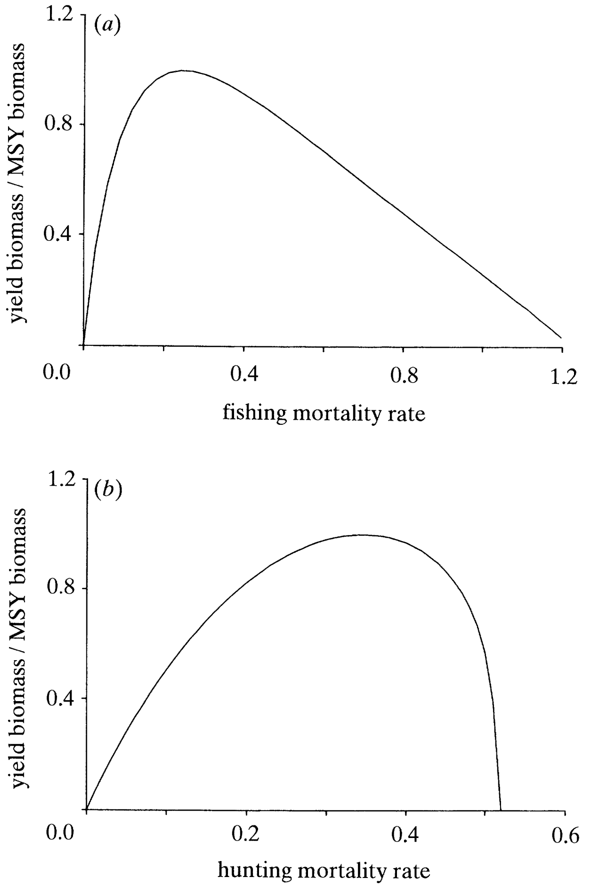


Figure 8. The response of the yield of red deer and herring to fishing (hunting) mortality. (*a*) Yield mortality plot for herring; (*b*) yield mortality plot for red deer.

There is one additional complication. Most fisheries models assume that once young fish are recruited a constant level of mortality applies. This is manifestly not the case for terrestrial mammals, indeed there is some evidence of an increase in mortality with age for certain fish (see, for example, Beverton & Holt 1957). Kirkwood *et al.* (1993) examined this problem using an average mortality rate that corresponded to a given age-dependent schedule. They used the well known formulation of Heinke (1913) and found that an erroneous assumption of constant mortality led to a small bias in estimates of yield for moderate increases of mortality with age. In terrestrial mammals this seems to be rather more pronounced and will be examined further elsewhere.

Comparison across species in the two environments now becomes a possibility. As an illustrative example we consider two species, red deer and herring. A stock and recruitment relationship for herring was fitted to Shepherd's (1982) model in Clark *et al.* (1985). This indicated a modest increase in recruitment with adult stock reduction. Using this relationship, in combination with the results derived above, it is possible to compare the two species. Both species have effectively similar lifespans, but the proportional yield of deer is

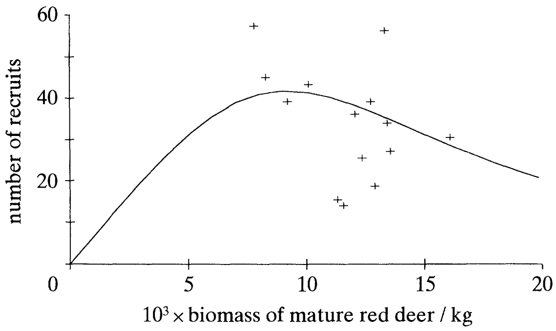


Figure 9. Stock and recruitment points derived from time series for red deer. Solid line, predicted recruitment of 2 year olds; crosses, observed recruitment of 2 year olds.

higher, almost double that of herring. This is not the whole story. In figure 8, the relationship between yield and the level of fishing or hunting mortality is given. This shows the way in which yield increases as mortality from exploitation increases, but shows also the way in which the yield decreases as the level of exploitation exceeds that which would produce the maximum yield. In the case of deer this decline is dramatic. In essence, what one is observing is the massive and immediate effects of the removal of breeding stock. Such effects are mitigated in the case of fish stocks by their massive basic fecundity. These results are unsurprising, indeed the demise of the unfortunately named common skate in the Irish Sea, documented by Brander (1981), well illustrates the fate of marine species which have a fecundity akin to that of terrestrial mammals.

5. VARIATION: ENVIRONMENTAL STOCHASTICY

The high level of variation of recruitment for given stock sizes in fish stocks is well known. Kirkwood *et al.* (1993) have examined the basic results on yield to allow for estimates of both the yield and measures of variation around that yield as a function of recruitment variability. At first sight, it is not clear whether the variation that occurs around the stock and recruitment relationship for terrestrial mammals is of similar dimensions to that observed for fish stocks. There are two possible ways of deriving this level of uncertainty around the basic stock and recruitment relationship. The first is to consider the uncertainty around the basic density-dependent relations that lead to its derivation. The second is, where it is possible, to observe that variation directly. Data to do this are relatively sparse and the only data set which appeared capable of manipulation into such a form is that for red deer on the Isle of Rhum. Figure 9 illustrates the stock and recruitment points that have been derived directly for red deer from that data and shows for comparison the deterministic curve collected from documented density-dependent responses. It is amusing to note that the level of variation around the recruitment relationship seems to be at least in line with that observed for fish species. There are numerous caveats around such a calculation and the intention here is merely to indicate that such data and treatment could usefully facilitate comparison of the variation of yield in the two environments.

6. MANAGEMENT

In the case of the exploitation of marine and terrestrial species there are critical differences in the way in which exploitation can be managed to maximize the yields.

In marine species this is usually done by altering the age at first capture. However, in terrestrial species it is possible both to further manipulate the age structure by effectively truncating the longevity of the species but, more importantly, to manipulate the sex ratio so that productivity is maximized for a given biomass, (Beddington 1974). The increases in yield that can be obtained by manipulating these variables are substantial, but beyond the scope of this paper.

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Discussion

R. J. H. Beverton (*Emeritus Professor of Fisheries Ecology in the University of Wales College of Cardiff, U.K.*). Professor Beddington commented on the dissimilarity between the typical yield-fishing curves in ICES assessment reports and those he derived. This may be because the ICES curves, which are mainly used for short-term catch forecasting, are on a yield-per-recruit basis. If, however, a stock–recruit relationship is introduced into these fishery models, and especially if, in addition, adult growth rate is reduced at high densities, the yield–F response becomes nearly symmetrically domed, similar in shape to those you presented for higher vertebrates.

The actual value of F at MSY depends, of course, on whether the species is slow growing and long-lived or fast growing and short-lived, but the ratio of F at MSY to the natural mortality coefficient, M, for the species in question is a remarkably robust statistic. In the original calculations with combined stock–recruit and density-dependent growth models that Sidney Holt and I did based on the North Sea haddock – a fairly long-lived species with a natural mortality coefficient of around 0.25–0.3 – F at MSY was about 0.45 to 0.55, i.e. about twice M. In recent studies on other single-species dynamics, both from models and empirically from the long-term data sets now becoming available, I am finding that F at MSY is between M itself for short-lived species and 2.5 M for long-lived ones. It would be interesting to know how these results compare with those of Professor Beddington for the higher vertebrates.

J. R. Beddington. The yield curve illustrated in figure 4*a* incorporates the stock and recruitment relationship. I believe the misunderstanding is due to our taking a somewhat higher age at recruitment than is traditionally done by ICES.

Professor Beverton's second point is intriguing. From the four examples that permit this analysis, the level of fishing mortality is in the range he suggests. However, I would comment that this is a substantial range.

J. Huisman (*Department of Plant Biology, University of Groningen, The Netherlands*). In his figures, Professor Beddington related recruitment to biomass and thereby incorporated intraspecific density dependence. In many natural ecosystems, however, recruitment is also seriously affected by feedback from other species such as prey and predators. I therefore wondered whether in his particular examples these interspecific interactions could perhaps be neglected or whether they should also be taken into account in order to arrive at a reasonable estimate of the maximal sustainable yield.

J. R. Beddington. Huisman is clearly correct that incorporation of interspecific effect is desirable. In much of the work presented here these are implicitly subsumed in the variation around the stock and recruitment relationship. However, where there is a strong link, for example between a prey and predator, maximization of yield for one depends on the level of yield taken from the other.