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EXAMINATION OF REDWINGED BLACKBIRD NESTLING GROWTH RATES USING THE LOGISTIC MODEL: A CASE FOR r AND k SELECTION?

M. I. Dyer
Natural Resource Ecology Laboratory, Fort Collins, Colorado

Z. Abramsky
Natural Resource Ecology Laboratory, Fort Collins, Colorado

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M.I. Dyer and Z. Abramsky[1]
Natural Resource Ecology Laboratory
Fort Collins, Colorado

One of the few processes of an avian population that presents the opportunity to collect sensitive information about the performance of that population is growth rates of young throughout the brooding period. Growth rate data are sensitive to many conditions of the breeding cycle: proximate influences, such as food availability and weather (Francis, et al., in prep.), and ultimate factors, such as species-specific characteristics, (Ricklefs, 1968). Additionally, the measurements themselves can be obtained with precision. The ability to make such detailed observations is extremely useful and is not always possible for other population parameters, such as determining life table data. Ricklefs (1967) gave considerable attention to this subject and elaborated techniques for making comparisons of growth rates of young of various bird species. From these, he and others (Fretwell and Bowen, 1974) have gone on to make several predictions about the status of various species and their populations in nature (Ricklefs, 1968, 1972, 1976).

Two parameters emerged from Ricklefs' work that are quite important for examining these processes: (1) the rate of growth $(g)^2$ of the young throughout the nesting period and (2) fledging weight (w) of the individual. Ricklefs (1967) presented three different curves which are useful to fit nestling growth data: the logistic, Gompertz, and von Bertalanffy equations.

To determine the growth function parameters, Ricklefs (1967) described a four-step graphical method of fitting the logistic equation to empirical weight data. Initially the asymptote of the growth curve is estimated; then the the growth data are recalculated as percentages of the estimated asymptote. For the third a conversion factor [= ¼ log (w/1-w) where w = percentage of the asymptote for each data point, see Ricklefs, 1967] is calculated and plotted as a function of time. In the final step the relationship resulting from step 3 is checked: if it follows a straight line, the growth rate (g) is calculated directly from the slope ($g = 4$ x the slope). However, if the estimated growth rate (g) does not follow a straight line, a new asymptote is determined and steps 1-4 are reiterated (see Ricklefs, 1967).

We were interested in investigating the hypotheses about intraspecific variability put forward by Ricklefs (1968) and in further determining the growth performances of the two major "populations" or "ecological races" (Mayr, 1963) of the Redwinged Blackbird (*Agelaius phoeniceus*), viz. marshland or wetland inhabitants and upland inhabitants. There have been reports about the possibilities of their distinctness (Dyer, 1964, 1968; Robertson, 1972, 1973a, b; Hesse and Lustick, 1972; Stone, 1973), and we wanted to test whether vital differences exist in growth rates of young in the nest between the two biotopes. Such differences, if existent, especially in adjacent regions, would indicate major differences in ecological associations in upland and wetland biotopes and perhaps genetic differences between the two populations.

METHODS

Testing of Logistic Models

Using Ricklefs' data (1967) we employed his suggested iterative method, but with differing estimates of the asymptote (30.0, 30.5, and 31.3) (Table 1). We then computed values of g to determine if the growth rates were dependent upon the initial estimates of asymptotes. Further, if N is the total number of days in the record, Ricklefs[1] method uses day N-3 (=14) for the basic calculations. To see if the final outcome was sensitive to this choice, we compared these results to the outcome using N-1, N-2, …, N 5. The growth rates obtained from these manipulations were tested for differences by a t-test (Table 2).

The second method we considered is a straightforward, nonlinear least squares (NLLS) fit for the logistic. We obtained F and R^2 values for testing the significance of model parameters. The R^2 is an estimate of one minus the correlation ratio (Wilks, 1962:86) and is not a linear correlation coefficient. In general, R^2 depends on the particular sequence of times b_y, …, b_n; it is not comparable between data sets if the times of observation are not comparable.

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[2] We prefer g to k (used by Ricklefs) because it avoids confusion between the constant proportional to rate of growth in individuals and K used by MacArthur and Wilson (1967) for population growth conditions, all within the context of the logistic model.

Data on which logistic model was applied. The data on Redwings, which were used initially to examine the performance of the two methods for estimating the logistic model, stemmed form several published reports and from Dyer (unpubl. data from Ontario, Canada) and Francis, et al. (unpubl. data of northern Ohio) (see Tables 3 and 4). As far as we know, all values were obtained from field programs where marked nestlings were weighed to the nearest 0.1 g on daily or on alternate-day schedules. Even though we had detailed original data from which to compute the logistic equation, we chose to uniformly use means of each day class throughout the nesting period so that those data reported in various literature sources could be utilized. For this report, we compare several examples of growth rate for males and females from Redwing marsh or wetland and upland habitats.

RESULTS

Comparison of Ricklefs' Method and Nonlinear Least Squares Method

We encountered difficulties with Ricklefs' method of computing the logistic values that gave us concern. When we computed the growth rate using his method and his data with three different asymptotes (30.0, 30.5, and the largest weight, 31.3), the resultant growth rates were significantly different (Table 1). This points out that Ricklefs' technique is sensitive to the first estimate of the asymptote and thus, biased. Furthermore, when we corrected the asymptotes (the conversion factors do not fall on a straight line; see Ricklefs, 1967) using his method (based on the adjustment of days N-2, …, N-5) for each asymptote, we obtained significantly different values (Table 2). This test also points out that Ricklefs' method is subjective, and the resultant growth rates are dependent upon (1) the first estimate of the asymptote and (2) if correction of the asymptote is needed, on the day from which the first asymptote estimate was made, (to correct the asymptote (N - (N-i) = i, where N = days used for full growth period and i = day chosen for correction). Exceptions were classes N-2 for asymptotes 30.0 vs 30.5 (NS); 30.0 vs 31.3, 31.3 vs 30.5 (p < 0.1); and N-3 asymptotes 31.3 vs 30.5 (NS). In order to see if correcting the asymptote according to day N-2 always yields consistent growth rate estimates or is just a coincidence, we examined several sets of Redwing growth data. In these cases the growth rates, which we obtained after correcting the asymptote according to day N-2, also were significantly different (p < 0.05).

In this respect we feel we have demonstrated a considerable amount of sensitivity in the method which is dependent upon several starting assumptions. This sensitivity is mainly due to the initial estimate of the asymptote and is easily a place where one can go wrong in attempting to compute growth rates with consistency.

To avoid these difficulties, we adopted a more objective method, viz. the NLLS method. By minimizing the sum of the squared deviaton of the fitted curve from the data, this technique finds the best estimates for growth rate and asymptote for any logistic growth data. The goodness of fit, as measured by R^2, for the blackbird data we have is never below 0.962 (Tables 3 and 4).

Growth Characteristics of Redwinged Blackbird Nestlings

The growth rates and asymptotic weights at the end of the nestling phase are given in Table 3 and Fig. 1 for 10 sets of Redwing data from wetland biotopes and 7 sets from upland biotopes. A comparison of growth rates of nestlings in these two biotopes using students' t-test show both the growth rates and asymptotic weights to be significantly different (p < 0.01, 15 df) (Table 3, Fig. 1). There are no demonstrable differences in _g_ between males and females (p > 0.1, 27 df), but there are quite obviously major differences between the asymptotes for estimates of fledging weights (p < 0.01, 27 df) (Table 4, Fig. 2).

DISCUSSION

Which to Use: Graphical Method or Nonlinear Least Squares?

Ricklefs (1967) provided a great service when he published his graphical method and doubtless many people have been able to use it satisfactorily. But because of the inherent problems involving qualitative assessments of the asymptote at the outset of the computational procedures, a step that is exceedingly critical in view of the sensitivity of the model, we felt that it was necessary to work with a less sensitive and more robust method, thus the recommendation of the NLLS approach. Since the two methods are conceptually different, it is not possible to make statistical comparisons of the results obtained from the two on a single set of growth data. In view of these difficulties and in view of the ease with which one can work with the NLLS, we feel it is not worth giving further regard to these comparisons. In short, we recommend outright use of the NLLS mehtod, because it can use all the data, minimize the mean square error components, and give all necessary parameters along with a goodness of fit evaluation; and, lastly, it is simple to use.

Comparisons of Redwing Growth Rates

Although it is not always stated explicitly in reports about Redwing growth, for our comparisons of wetland and upland growth parameters we have assumed that the data sets con-

tained 1:1 ratios of males and females. Such conditions hold for the Ontario and Ohio data. But even if there were not (because no difference exists between male and female growth rates), it is apparent that there are major differences in the growth rates (*g*) of Redwing nestlings from wetland and from upland biotopes (Fig. 1).

The conclusion is counter to that of several other wetland-upland comparisons (Brenner, 1964; Holcomb and Twiest, 1970; Robertson, 1973a), which stated that growth rates are not different for the two populations. These reports, however, were results of employment of linear and exponential models to analyze conditions for single areas, while we are comparing the growth performance of several populations scattered in space and time using a more appropriate model for interpretation of growth parameter performance.

One of the predictions made by Ricklefs (1968) was that growth rates should vary intraspecifically by no more than 30% (p. 423) or 20% (p. 447). To evaluate this condition for the Redwing, we have selected *g* values from Tables 3 and 4 and have compared their performance (Table 5). From these we see examples of considerable variation from place to place and from year to year as well as examples of substantial consistency. For instance, *g* values of Kent County, Ontario, Canada (Dyer, unpubl. data) and Spokane County, Washington, populations (Haigh 1968) differ by 60%. But a comparison between years within a single Ohio marsh shows a difference of only 3.8% (Francis et al., unpubl. data). Variations of a smaller magnitude are noted within and between areas for upland ecological types (Table 5). The greatest difference is between the lowest growth rate of wetland and the highest growth of upland (73.7%); the means of all populations differ by 13.2%. Difference in the growth rates for females between populations is 34.9% whereas for males it is 26.7%. Differences of 31.5% for females and 27.7% for males exist within an Ohio marsh between years. Comparisons for *g* for all males to all females show less than 1% variation. Thus, it is apparent that there is a great degree of flexibility in the Redwing growth rates in response to possible phenotypic or genotypic differences and certainly in the way they respond to local variations in macro- and micro-climate (Francis et al., unpubl. data).

From comparisons made of *g* (Table 4, Fig. 2) using the NLLS model, it is apparent that there are no growth rate differences between males and females; the only real difference is the asymptote. This observation predicts that the energy being delivered to each fledgling, no matter which sex, is being processed in much the same manner but that sex-specific controls (endocrine growth compounds?) provide differing limits to final weights at the end of the nestling growth phase. There is the possibility that females tend to mature and fledge earlier than the males, but this has not been studied conclusively. Some hint of this fact is provided by comparing the estimated fledging weights with reports of weights of adult birds that were held in outdoor cages throughout the winter in Ontario (Lewies and Dyer, 1969). According to these estimates, males tend to achieve 42% of their adult weight before fledging, whereas females achieve 32%. Even though these percentages are not adjusted allometrically for this sexually dimorphic species, it is probable that males achieve a weight advantage in contrast to the females before they leave the nest to start foraging on their own.

It has been suggested several times (Dyer, 1964, 1968; Parker, 1968; Hesse and Lustick, 1972; Stone, 1973) that these two "ecological races" have distinct characteristics. For instance, Dyer (1968) and Parker (1968) showed that nestlings from wetland biotopes achieve homeothermy faster and apparently operate physiologically on different substrates, their R.Q. being higher than upland nestlings. These observations, coupled with our findings of slower growth rates and higher asymptotes in wetland birds, in contrast to upland birds, create a consistent picture. We present the hypothesis that faster growth rates, slower achievement of homeothermy, independence at a lower weight, development, and apparent use of fat substrates for metabolic fuel are examples of *r*- selected processes giving an advantage for growth and development in harsh environments, the upland biotope; whereas slower growth, faster achievement of homeothermy, fledging at higher weights, and utilization of fuels indicative of higher R.Q. are examples of *k*-selected processes in a more stable and predictable environment, namely marshlands.

In addition to our evidence of differences of nestling growth rates following *r* and *k* patterns (MacArthur and Wilson, 1967), Case and Hewitt (1963) suggested that there are more eggs laid per clutch and more nestlings raised per nest in uplands than in marshland biotopes. These responses fit criteria proposed by Pianka (1974) as satisfying *r* and *k* selection. It is also apparent that several other features known about Redwing morphology fit Pianka's criteria. Dyer (1964), from a study in South Dakota, showed that upland males weighed significantly less than marshland males, though there was no difference in the weights of females. Stone (1973) reported that Ohio marshland males were significantly longer than upland males, suggesting that overall body size is larger as a consequence.

Both Dyer (1964) and Stone (1973) reported statistically significant differences in many other characters: Dyer showed that culmen and nostril tip were longer in upland males, and Stone reported longer culmen lengths for upland females; bill depth was greater for

marsh females than for upland females in South Dakota (Dyer, 1964). Dyer also reported that gape angle was larger for upland males than for marshland, and that the angle of the maxilla-jugal bones was significantly larger for both male and female upland birds, compared to marshland birds. This latter point may be quite important, for it follows the hypothesis of Beecher (1951) that adaptations of these bill components in icterid species are closely correlated with ability to capture insects or crush seeds: the larger gape and bone junctures better equip the bird for capturing flying insects, and the converse is true for handling heavy seeds. Further, Stone (1973) lists a whole series of morphometric parameters which show differences between the two ecological races, but not all of them are interpretable in this context. For instance, he found that upland males had greater relative (on the basis of mean character value divided by the cube root of the weight) organ weights than marshland males, but the converse was the case for many organ weights of females; thus, it is difficult at this stage to attribute any function to these measurements.

Of more speculative nature is a listing of *r* and *k* attributes estimated to exist following predictions from Pianka's (1974) theoretical approach. As many of these as can be ascertained at this time are shown in Table 6. For the most part, except for the attributes this paper addresses on development, there has been little or no systematic screening of the population parameters presented here. Thus we emphasize that all the attributes and their estimated responses simply form hypotheses which need rigorous testing, either from collection of new data, or from design of experiments that will give the necessary information to determine whether our proposal of *r* and *k* assignment is tenable.

While we suggest that our data fit *r* and *k* selection theory on nestling growth rates and weight at fledging expectations very well, it is difficult to translate these phenomena into selection at the individual level. Goodman (1974) discussed Lack's (1954, 1966) hypothesis concerning the role of natural selection on clutch size and probability of fledging success per egg distributed over clutch size and concluded that there are likely *r* and *k* features important to the population. We suggest that the material presented by Case and Hewitt (1963) showing tendency for larger clutch size in uplands, our data showing faster growth and lower weights at independence, and the tendency to keep this size differential as adults relate to definitions of differences in fitness of young between the two ecological races. If this hypothesis is correct, it may be possible to find differences of life table characteristics between these two ecological races in the future. Robertson (1972) argued for the wetland biotope as being optimal, but Wiens and Dyer (1975) challenged some of his assumptions on the basis that the bulk of the population is raised in the upland biotope.

Currently then most of the members within the eastern North American population have been raised in what to this point has been considered the less desirable of the two biotopes. The survival value for upland nestlings to "grow faster and fledge earlier," or at least fledge at lower weights, might be explained energetically. The female parent would be released from a heavy strain of feeding older, heavier birds in the nest. This would be especially true if food is harder to obtain in uplands contrasted to marshlands. These growth responses would also be selected for by presence of predators routinely foraging through the upland areas. Quicker growth and earlier independence would make the young less susceptible to heavy predation pressures. The converse of this picture, i.e., slower growth and greater fledging weights in marshlands, is less clear. The question yet remains, why are there these differences? Common knowledge about this situation states that the ancestral home of the Redwing is in marshland biotope, but now there is growing cause to wonder if this "common knowledge" is correct.

Finally we suggest that if our hypothesis about such population differentiation with the Redwing species is shown to be correct with subsequent testing, at least eastern North American populations can be defined as in Fig. 3. This hypothesis is in itself a modification from that proposed by Pianka (1974). Here we suggest that along the *r* and *k* continuum, upland populations tend to be more *r*-selected and wetland populations more *k*-selected, even though we cannot now tell where these points are along the continuum.

Should this proposal withstand rigorous testing, it can have important meaning to management. The first thought to come to mind is that Redwinged Blackbirds are well adapted to adjust population numbers as a direct response to changes in selection pressures in either major habitat. Thus, it is possible that Redwings can withstand considerable increases in yearly mortality and compensate for losses by adjustments on the breeding grounds. However, it is equally possible that "rebound" levels may result, or perhaps even that Redwings have reached the "limits" of their capacity to compensate for changes in nominal mortality. Such statements, of course, hold for any animal species; our work only suggests an additional level of complexity in that before natality-mortality parameters on a continental scale can be obtained for Redwings, management agencies must consider obtaining such important information in more than one resource habitat. To fail to do so can only lead to potential costly disaster following major attempts to manage this species and resource problems associated with it.

SUMMARY

A critical examination is given to basic assumptions and ease of computing growth rates (g) and asymptotes using logistic models. A graphical method (Ricklefs, 1967) and a nonlinear least square (NLLS) method are compared. The NLLS is recommended for general use, because it is least subjective and gives the fewest problems. Using this approach growth data from various Redwinged blackbird populations are compared. The results show that there are differences in growth rates (g) and asymptotes (w) when comparing wetland and upland populations; g is higher for upland populations and w is lower. There are no differences between male and female growth rates, but there are obvious differences in w, and thus fledging weights, between the sexes of this dimorphic species.

These results have been interpreted to mean that upland nestlings may derive a selective advantage by growing faster and fledging with smaller weights. This strategy would release the female from heavy demands for feeding the nestlings longer, in contrast to the situation that apparently exists in wetlands where food supplies may be more plentiful and growth rates of young slower. It would also be advantageous for upland nestlings to spend less time in the nest because it is generally felt predation is higher in upland conditions. These conditions are interpretable in the context of MacArthur and Wilson's (1967) theory of r and k selection; the upland ecological race has the tendency of an r strategist; the wetland, a k strategist.

ACKNOWLEDGEMENTS

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COMMENT

[Editor's note: Questions ware not discernable on the tape, but the comments by the speaker are of sufficient value to be Included alone.]

What I propose to do, if I get enough courage, is to perform a series of experiments to examine whether these growth rates are phenotypically or possibly genotypically determined.

Gordon Orians has worked a great deal on polygyny, and as I recall his very elegant model indicates that the female selects the type of association based on the goodness of habitat.

Thus polygyny is favored in the more productive habitats which are in the wetlands, and the polygyny ratio should be higher in the more productive areas; and I think that has been borne out. If I'm correct, that really lends some interesting complications to the problem, because then you have to know on a continental or at least a regional scale what the sex proportions are in the uplands and the marshlands to be able to sort out this problem. We've got a long way to go on it.

I know Sheldon Lustick's study well, and I think it's a very important study for this hypothesis. For a while his study created an enigma for me. The geneticists right now, going back to Dobzhansky's work, are really in a quandry as to what variation means in two different genotypes. There is a publication about two years old that examines Dobzhansky's original data on the fruit fly distribution across the midwest and has come up with exactly converse findings to what's accepted in current dogma, so it's a wide-open question at this particular time. I can't answer the genetics; I'm more interested in the ecological factors, because I think there's a potential for ecological selection. Thus I think Lustick's work fits new developments in genetic theory.

The one weak link in the model has been pointed out by several people. I think I can explain why faster growth rates and low fledging weights should be advantageous to the upland population. I cannot explain the converse of why there should be a selection preference for slower growth rates and higher fledging rates. I don't know what the selection pressures are. If you're selecting for something you get one answer. If you select against something, you get another answer. I'm not sure we're selecting for anything.

I think Gordon Orians is currently working on a theory that large body size is selected for and is an advantage on the breeding grounds because of being able to attract more females. But Heidi Good and Dan Johnson working at Rice University have come up with some intriguing evidence to show that in the wintering grounds the big male is the first one selected against.

The Information I have on body size collected in South Dakota shows that the wetland males fledge at a higher weight and maintain that weight advantage all through life in the wetlands. So things are starting to fit together fairly well, but I'd like to have a lot of other tests on this hypothesis.

The only other evidence that I know of is a case in Huron, Ohio. There in a 2-year study, if you look at both years, there's no difference between the upland nesting and the marshland nesting. But if one looks at one of the years it fits this theory very nicely. Another warning is that we shouldn't try to get a Procrustean fit of everything. I think there are going to be some neutral factors, but I don't know which ones. We simply do not have enough evidence to make such judgements.

TABLE 1. Comparison of growth rates (*g*) using iterative graphical method (Ricklefs 1967) with three estimates of the asymptote and four alternate-day class corrections. If no bias exists in this method, it would be expected that there would be no difference between mean growth rates predicted for each asymptote. *t*-tests were used to make the comparisons (see text).

Growth rates	Values of *g* received using various asymptote estimates		
	30.0	30.5	31.3
First estimates of growth rates (N)	0.520	0.434	0.363
Corrected estimate of growth rates (N-2)	0.468	0.462	0.388
Corrected estimate of growth rates (N-3)	0.496	0.394	0.366
Corrected estimate of growth rates (N-4)	0.570	0.391	0.344
Corrected estimates of growth rates (N-5)	0.517	0.381	0.324
Mean[1]	0.514 ± 0.037	0.410 ± 0.031	0.357 ± 0.024

[1]/ 30.0 vs. 30.5 $t = 4.783$ 8 d.f. $P < 0.01$
     30.0 vs. 31.3 $t = 7.881$ 8 d.f. $P < 0.01$
     30.5 vs. 31.3 $t = 3.049$ 8 d.f. $P < 0.01$

TABLE 2. Probability levels of *t*-tests comparing growth rates of Ricklefs' (1967) example when selections are made of differing asymptotes. Adjustments of asymptotes and slopes are made on days N to N-5 (see text).

Day Class	30.0 vs. 30.5	30.0 vs. 31.3	31.3 vs. 30.5
N	0.05	0.001	0.05
N-2	NS	0.1	0.1
N-3	0.01	0.02	NS
N-4	0.01	0.001	0.05
N-5	0.001	0.001	0.02

TABLE 3. Summary of Red-winged Blackbird growth parameters. The data are presented for available reports by two habitat types: wetland nesting areas and upland nesting areas.

Area	Year	Source[1]	g	Asymptote	R^2
Wetland Habitat					
Kent County, Ontario Bradley's Marsh	1955	1	0.3240	50.50	0.974
	1956	1	0.4574	35.72	0.966
	1957	1	0.3921	39.06	0.984
Erie County, Ohio	1971	2	0.4707	39.40	
	1972	2	0.4535	37.60	0.990
Toledo, Ohio	1955	3	0.3845	40.40	0.988
Battle Creek, Michigan	1955	3	0.4332	41.02	0.985
Spokane County, Washington	1955-67	4	0.5184	40.12	0.999
New Haven, Connecticut	1970	5	0.4715	36.50	0.999
Ohio	1940	6	0.4949	37.30	0.996
Mean ± S.E. [2]			0.4400 ± 0.0582	39.75 ± 4.160	
CV =			41.63	33.09	
Upland Habitat					
Kent County, Ontario Bradley's Farm	1966	1	0.5373	35.63	0.983
Erie County, Ohio Mason Road, Old Field	1971	2	0.5234	34.80	0.996
	1972	2	0.4054	40.02	0.978
Plum Brook, Old Field	1971	2	0.5627	33.9	0.999
	1973	2	0.5474	34.89	0.996
Toledo, Ohio	1964	3	0.4979	36.3	0.998
New Haven, Connecticut	1970	5	0.5124	34.3	0.992
Mean ± S.E. [2]			0.5124 ± 0.0519	35.69 ± 2.069	
CV =			26.00	15.34	

[1] 1: Dyer, unpubl. data; 2: Francis and Dyer, unpubl. data; 3: Holcomb and Twiest, 1970; 4: Haigh, 1968; 5: Robertson, 1973a; 6: Williams, 1970.

[2] Means of wetland and upland habitats are significantly different, $p < 0.01$, 15 df, ($t = 2.63$).

TABLE 4. Summary of Red-winged Blackbird growth parameters for males and females. Data are from several published and unpublished sources.

Area	Year	Date	Source[1]	σ	Asymptote	R²
females						
Kent County, Ontario Bradley's Marsh	1965	May-June	1	0.4504	33.42	0.962
Erie County, Ohio						
Sawmill Creek Marsh	1971	May	2	0.6074	30.4	0.994
Sawmill Creek Marsh	1971	June	2	0.4620	29.2	0.994
Sawmill Creek Marsh	1972	May-June	2	0.5678	29.9	0.999
Plum Brook Old Field	1971	May	2	0.6050	30.08	0.909
Plum Brook Old Field	1971	June	2	0.6026	30.9	0.997
Plum Brook Old Field	1973	May-June	2	0.5224	30.01	0.996
Mason Road Old Field	1971	May	2	0.4559	31.0	0.993
Mason Road Old Field	1971	June	2	0.4509	37.4	0.999
Mason Road Old Field	1972	May-June	2	0.5196	32.1	0.997
Toledo, Ohio	1904	--	3	0.5680	30.3	0.999
	1965	--	3	0.5276	29.2	0.998
Battle Creek, Michigan	1965	--	3	0.5731	30.9	0.998
Spokane County, Washington	1965-67	--	4	0.5286	33.7	0.999
Ohio	1940	--	5	0.4294	33.7	0.996
Mean ± S.E.[2]				0.5229 ± 0.0649	32.53 ± 2.226	
CV =				48.07	27.34	
males						
Kent County, Ontario Bradley's Marsh	1965	May-June	1	0.4857	44.7	0.996
Erie County, Ohio						
Sawmill Creek Marsh	1971	May	2	0.5420	41.04	0.996
Sawmill Creek Marsh	1971	June	2	0.6150	39.9	0.997
Sawmill Creek Marsh	1972	May-June	2	0.4815	39.2	0.998
Plum Brook Old Field	1971	June	2	0.5043	41.3	0.999
Plum Brook Old Field	1973	May-June	2	0.5503	39.6	0.999
Mason Road Old Field	1971	May	2	0.5195	37.9	0.986
Mason Road Old Field	1971	June	2	0.6422	41.6	0.999
Mason Road Old Field	1972	May-June	2	0.5130	38.4	0.986
Toledo, Ohio	1964	--	3	0.5408	40.7	0.998
	1965	--	3	0.4897	40.1	0.999
Battle Creek, Michigan	1965	--	3	0.5206	41.9	0.994
Spokane County, Washington	1965-67	--	4	0.5184	46.5	0.999
Ohio	1940	--	5	0.5503	41.3	0.997
Mean ± S.E.[2]				0.5304 ± 0.0383	41.02 ± 2.295	
CV =				27.02	20.93	

[1] 1: Dyer, unpubl. data; 2: Francis and Dyer, unpubl. data; 3: Holcomb and Twiest, 1970; 4: Haigh, 1968; 5: Williams, 1970.

[2] Means of female and male growth rates are not significantly different (t = 0.293, p > 0.1, 27 df). Means of female and male asymptotes are significantly different (p < 0.001, 27 df).

TABLE 5. Selected comparisons of extremes in growth rates shown in tables 3 and 4. We show percentages by which fastest growth rates *(g)* exceed slowest for the various categories

Category of comparison	Range of g	%$	Intraspecific comparison
Within wetland populations, All birds	0.324 to 0.5184	60.0	Ontario to Washington (approximately same year, see Haigh 1968).
	0.324 to 0.4574	41.2	Within Ontario, between years.
	0.4535 to 0.4707	3.0	Within Ohio, between years.
Within upland populations, All birds	0.4054 to 0.5373	32.5	Ohio to Ontario, between years.
	0.4054 to 0.5627	38.8	Within Ohio, between years.
Between wetland and upland populations	0.3240 to 0.5627	73.7	Ontario to Ohio, between years.
	0.440 to 0.4982	13.2	Between wetland and upland means for all areas and all years.
Within all females	0.4504 to 0.6074	34.9	Between Ontario marsh and Ohio marsh, between years.
	0.4620 to 0.6074	31.5	Within Ohio marsh, between years.
Within all males	0.4851 to 0.6150	26.7	Between Ontario marsh and Ohio marsh between years.
	0.4815 to 0.6150	27.7	Within Ohio marsh, between years.
Between males and females	0.5229 to 0.5278	1.0	Means of all males to means of all females, between areas and years.

TABLE 6. *r* and *κ* correlates estimated for two Red-winged Blackbird ecological races (after Pianka 1974).

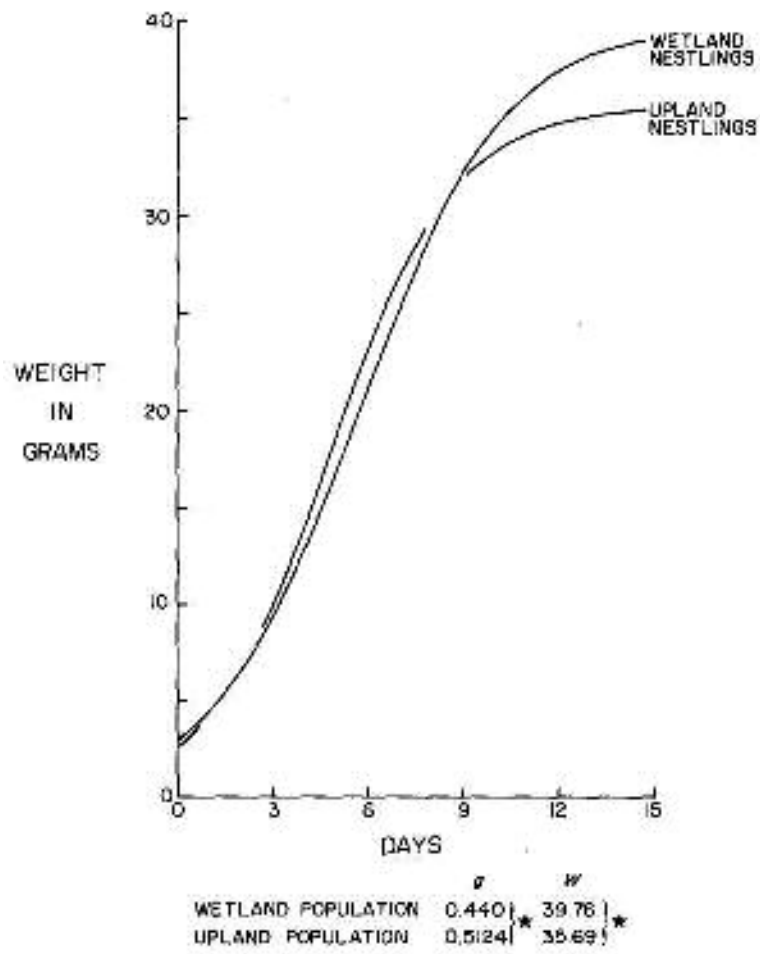| r and κ correlates	r theory	Upland observations	κ theory	Wetland observations	Authority
Climate					
Variable, uncertain	+	⊖	-	⊖	Author's
Predictable	-	⊕	+	⊕	estimate
Mortality					
Catastrophic (density indep)	+	?	-	?	Pianka, 1974
Density dependent	-	?	+	?	
Survivorship					
Type III	+	⊕	-	+	Deevey, 1947
Type I and II	-	⊖	+	-	
Population size					
Variable in time	+	⊖	-	⊖	Dyer et al.,
Constant in time	-	⊖	+	⊕	1972
Competition					
Interspecific severe	-	⊙	+	⊙	Pianka, 1974
Selection favors					
Rapid development	+	⊖	-	⊖	This paper
Slow development	-	⊕	+	⊕	This paper
High z max (growth rate)	+	⊕	-	⊖	Author's est.
Greater competitive ability	-	?	+	?	--
Early reproduction (life stage)	+	?	-	?	--
Delayed reproduction	-	?	+	?	--
Body size					
Fledgling lower	+	⊕	-	⊖	This paper
Fledgling higher	-	⊖	+	⊖	This paper
Adult lower	+	⊖	-	⊖	Dyer, 1964
Adult higher	-	⊖	+	⊕	Dyer, 1964
Number of broods					
Single	-	- to +	+	- to +	Authors' est.
Multiple	+	⊕	-	+	Authors' est.
Length of life					
Short (less than 1 year)	+	-	-	-	Finkhauser 1967
Long (greater than 1 year)	-	+	+	⊕	Dyer et al., in press
Productivity per female					
High	+	⊕	-	⊖	Dolbeer, 1976
Low	-	⊖	+	⊕	
Productivity per unit area					
High	-	⊖	+	⊕	Dolbeer, 1976
Low	+	⊕	-	⊖	Dolbeer, 1976
Productivity vs. efficiency					
High	-	?	+	?	--
Low	+	?	-	?	--

Fig. 1.   Plot of mean North American Red-winged Blackbird growth
           curves for two habitat types. Population means for growth
           rate (g) and asymptote at fledging (W) are significantly
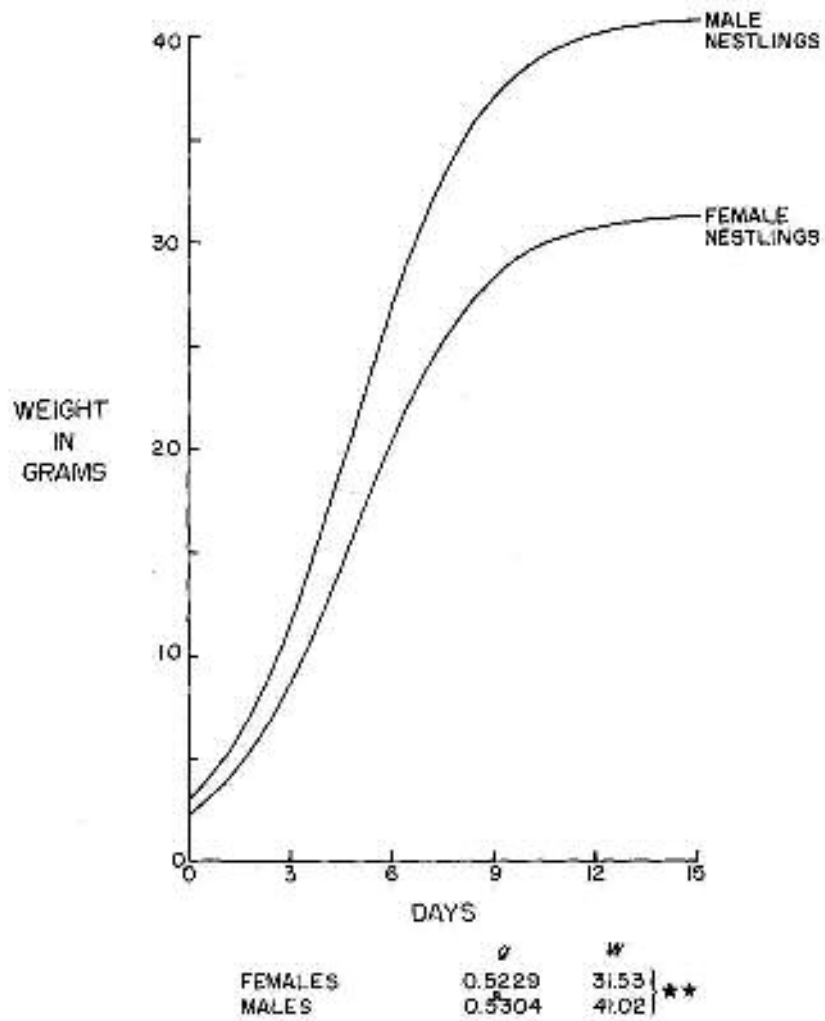   different (p < 0.05, see Table 3).

Fig. 2. Plot of mean North American Red-winged Blackbird growth curves for males and females. Growth rates (g) are not different (p > 0.1) whereas fledging weights (W) are significantly different (p < 0.05) for this dimorphic species (see Table 4).

r

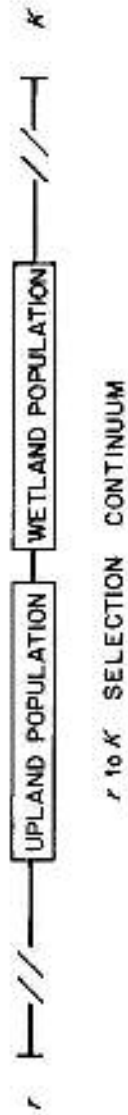UPLAND POPULATION | WETLAND POPULATION

K

r to K SELECTION CONTINUUM

Fig. 3.   Hypothetical case involving Pianka's (1974) r to K continuum. Two discrete populations of Red-winged Blackbirds are considered, one an r-selected type that inhabits uplands and the other a K-selected type that dwells in wetland breeding areas.