REP 1995-092

1995. in D. Rollins, C. Richardson, T. Blankenship, K. Canon, and S. Henke (Eds). Proc. Symp. Coyotes in the Southwest: a compendium of our knowledge. Texas Parks and Wildl. Dept., Austin. 180 pp.

THE EFFECTS OF CONTROL ON COYOTE POPULATIONS: ANOTHER LOOK

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Abstract: Population dynamics models are useful for estimating coyote (*Canis latrans*) population responses to exploitation as well as to hypothetical birth intervention techniques. At least 6 coyote simulation models have been developed over the past 25 years. This paper reviews the model developed by Connolly and Longhurst (1975), and identifies some potential improvements based upon new biological information and modern computing technology. The biological concepts embodied in the Connolly-Longhurst (C-L) model seem as valid in 1995 as they were in 1975. Newer studies have tended to reaffirm rather than revise earlier concepts of coyote population mechanics. One significant shortcoming of the C-L model, as acknowledged by the authors at the time, was its failure to include immigration as one of the mechanisms for replacement of coyotes removed in control. Subsequent studies have reiterated the importance of immigration and emigration in the dynamics of exploited coyote populations, but researchers have not made corresponding progress toward the incorporation of these phenomena into simulation models. Updating the C-L model would consist largely of revamping it to run on modern computers and software. A new edition would make the model useful to wildlife managers interested in the effects of predator control on the dynamics of selected coyote populations. The updated model would calculate births and deaths monthly rather than annually, and minor changes could be made to the birth and natural mortality functions. However, the revised model probably would sustain most of the conclusions stated in 1975.

The coyote is much admired for its survival ability. As Gabrielson (1951) recognized many years ago, no other American mammal has shown greater adaptability and stamina in the face of ruthless oppression. In spite of guns, dogs, poisons, and traps, pursued by hired hunters and carrying a price on his head, the coyote has managed not only to survive but to extend his range into new territory. Hundreds of thousands of coyotes are killed each year in the western United States, yet large and healthy populations remain.

How does the coyote do it? The biological answers to this question have been sought in many field studies of coyote populations (Connolly 1978). Additionally, several teams of biologists have analyzed the elements of coyote population dynamics and assembled them into mathematical simulation models of coyote populations.

The models that help us understand the coyote's legendary survival ability are those that provide numerical estimates of coyote population responses to management; i.e., exploitation (killing or harvest) and birth control. At least 4 such models were developed in the 1970s (Connolly 1978). This paper reexamines one of these models (Connolly and Longhurst 1975; hereafter termed the C-L model) in light of more recent information. Herein I identify some improvements that, if implemented, would update the model and make it more useful to wildlife managers.

The C-L model

The C-L model established an initial population 100 coyotes. Coyote numbers in this population changed over time due to births, "control kill" (defined later), and natural losses. The model was developed for the purpose of estimating the probable effects of exploitation, birth suppression, or both on coyote populations.

Simulation experiments with the C-L model showed that the primary effect of killing coyotes was to reduce coyote population density, thereby stimulating density-dependent changes in natality and natural mortality rates. The simulated population survived indefinitely when 70% of its members were killed annually, but declined to zero in about 50 years when 75% were killed each year. Coyote populations reduced by intensive control returned to pre-control densities within 3-5 years after control was terminated.

In the C-L model, birth suppression as the sole management tactic reduced the coyote population significantly only when most (80-95%) of the females were prevented from producing pups. Birth suppression combined with killing appeared to be more effective in reducing coyote numbers. The model and its use to determine population responses to various control strategies were described in detail by Connolly and Longhurst (1975)[1].

The C-L model revisited: assumptions, input parameters, and computations

Population stability. In the absence of control or exploitation, the C-L model's coyote population was stable, both in numbers and age structure. The carrying capacity of the environment also was stable and did not change regardless of the level of exploitation. These principles would be retained if I was updating the C-L model.

Area inhabited by the coyote population. The population inhabited an area of unspecified size, but with sufficient resources to sustain a breeding population of just 100 coyotes each year. The carrying capacity of this area was assumed to be constant year after year. In updating the C-L model, I would now make it functional with geographic areas of any desired size. The size of the area, together with an estimated coyote density, would be specified with other initial input parameters at the start of each run. The initial coyote population would be the product of coyote density and geographic area. For example, an initial input of 1,000 mi^2 with a density of 1.5 coyotes/mi^2, would yield an initial population of 1,500 coyotes.

Number of age classes. All coyotes in the C-L model were either pups (0-12 months old) or adults (over 12 months old). Pups approaching their first birthday were termed yearlings for purposes of birth computations. Adults were not tracked as yearly age classes, so natural death rates were constant for adult coyotes of all ages. In the updated model it would be desirable to track individual cohorts up to 8 or 10 years of age.

Causes of death. In the C-L model, all coyote deaths resulted from either control (killing by humans) or natural causes (all non-human causes). This would not change in the updated model.

Control kill specifications. A "control kill" rate was specified as one of the initial input parameters for each run of the C-L model. Control kill was specified as a percentage of the maximum (post-whelping) population, and the same percentage was applied to pups and adult coyotes. It was not possible to take different proportions of different age classes nor to distribute the control kill among different seasons of the year. An updated model could permit the control kill to be specified separately for each month, with zeros entered for those months when no kill would occur. Control specifications could be entered as either percentages or number of coyotes to be removed from each age class.

Birth control specifications. Birth control in the C-L model was simulated by preventing specified percentages of the normally-breeding females from having litters. This procedure would be retained in the updated model, and I would add the ability to specify birth prevention as either percentages or numbers of females in each age class. The pragmatic reader may note that practical birth control methods for wild coyote populations are no nearer to realization now than they were 20 years ago. Therefore, the simulation of birth intervention impacts has little relevance to coyote management as practiced in 1995.

Birth and death computations. Each annual cycle in the C-L model consisted of one computation of births, followed by a single computation of control removal (if any) from the maximum (post-whelping) population, followed by a single computation of natural mortality. Natural mortality rates were applied to those coyotes that survived control. At the end of each year, the closing population became the beginning (breeding) population for the next year. Seasonal differences in control or natural mortality rates could not be simulated in the C-L model.

The updated C-L model would perform calculations monthly rather than annually. Births could all occur in 1 month, as in the C-L model, or could be distributed across 2-3 months as they actually occur in most wild coyote populations. The distribution of births would be specified in the initial

[1] *This publication can be obtained from the Denver Wildlife Research Center, P.O. Box 25266, Denver CO 80255.*

input. Control kills would be subtracted in the month(s) specified in the initial input.

Natural mortality in the updated model would be subtracted in each month, unless the model user specified no natural mortality for the month. Users would have the option of specifying the proportion of total annual natural mortality that would occur in each month separately for each age class. If no distribution was specified in the initial input, the model would automatically distribute the total annual natural mortality evenly over the 12 months of each year.

In the revised model, the computation sequence each month would proceed as follows:

OPENING INVENTORY
+ *BIRTHS (if any)*
- *CONTROL KILL (if any)*
- *NATURAL MORTALITY (if any)*
= *CLOSING INVENTORY.*

The closing inventory each month would become the opening inventory for the next month. Each set of 12 months in the model would comprise one annual cycle. Monthly statistics would be summed as necessary to produce annual statistics.

Sex ratios. Even (i.e., 50 males:50 females) sex ratios were assumed in the C-L model for each age class, including pups at birth. All mortality, whether from control or natural causes, applied to males and females equally. Other coyote population models reviewed by Connolly (1978) also assumed a 50:50 sex ratio, as did more recent simulations (Sterling et al. 1983; Windberg and Knowlton 1988).

More recent field studies, however, have been inconsistent on this point. Some reported even sex ratios (Nellis and Keith 1976; Crabtree 1989), but others suggested that there was a preponderance of males among samples of adult coyotes from populations where exploitation was low (Gese et al. 1989) or a preponderance of females where exploitation was more intense (Knowlton 1972). Therefore, it is not clear to me whether an updated C-L model should or should not incorporate sex differential birth or death rates. It would be easy enough to incorporate sex-differential birth or mortality functions into the model, but difficult to develop valid sex-differential functions from information currently available. Considering all current information, I probably would retain even sex ratios as in the C-L model.

Compensatory natality and mortality. A key assumption in the C-L model, and in all other coyote population models known to me, is the principle of compensatory natality and mortality. That is, removal of coyotes enhances conditions for the animals that survive exploitation so that birth rates are higher and natural mortality lower than in the unexploited population. These phenomena were simulated in the C-L model by density dependent functions; i.e., equations that caused average litter size, proportions of female coyotes producing young, and proportions of animals dying of natural causes to vary with relative coyote density (Figs. 2-4 in Connolly and Longhurst 1975).

A few reports published since 1975 have reiterated the existence and importance of compensatory or density dependent relationships in coyote population dynamics (Connolly 1978; Sterling et al. 1983). Variations in emigration rates also may be density dependent (Knowlton and Stoddart 1983). Thus, the assumption of density dependent compensations in birth and death rates appears to be as valid in 1995 as it was in 1975.

Explicit quantification of the magnitude of these compensatory responses, however, was lacking in 1975 and remains equally lacking in 1995. Connolly and Longhurst (1975) presented birth and death rate functions as speculative and pointed out a need for additional research to refine them. The C-L model was constructed so that improved functions could readily replace the initial ones. As of 1995, however, improved functions have not been forthcoming, and the specific forms of these functions remain a matter of speculation. If further work is done with the C-L model, sensitivity analyses would be desirable to determine how much the model output is affected by changes in the shapes and slopes of these functions.

Birth rate functions. The C-L model contained 3 density-dependent birth rate functions (Connolly and Longhurst 1975:Figs. 2-3). Two of these expressed the relationship between relative population density and the proportion of adult females and yearling females, respectively, that would produce litters. The third function established mean litter sizes that varied with relative population density. In the C-L model, mean litter size for yearling females was the same as that for adult females. The shapes of these functions were highly speculative, but there is little

new research that would help refine them.

The C-L functions for yearling and adult pregnancy rates were concocted from published estimates of the ranges of variation in pregnancy rates, i.e., 0-70% for yearlings and 60-90% for adult females. Subsequent studies have tended to yield pregnancy rates that fall in or near these ranges. Nellis and Keith (1976), for example, found pregnancy rates of 94% for adults and 14% for yearlings in central Alberta. Examinations of female coyotes from a lightly exploited population in southeastern Colorado showed that all 10 adults contained placental scars, but none of 11 yearlings showed evidence of whelping (Gese et al. 1989). Crabtree (1989), in contrast, found that alpha females aged 2-6 years were the most successful breeders in an unexploited coyote population in eastern Washington; overall, 40% of his females were productive and the age at first breeding was 2-3 years.

These studies do not indicate a need to revise the yearling or adult pregnancy rate functions in the C-L. Consequently, I would not change them in an updated model.

Mean litter sizes also have been estimated in several studies published since 1975. Nellis and Keith (1976) reported an average of 5.3 pups/litter for 26 litters examined at dens in Alberta. In northern Utah, mean litter sizes were estimated to vary in different years from less than 5 to more than 8 pups per litter based on placental scar counts; mean litter size was correlated with jackrabbit (*Lepus californicus*) abundance (Knowlton 1989). The model of Sterling et al. (1983) assumed mean litter sizes to range from 4.3-7.6 pups/litter. The lightly exploited Colorado population of Gese et al. (1989) had an average of 3.2 pups/litter (n = 16), whereas an average of 5.6 pups/litter was reported from an almost unexploited Washington population (Crabtree 1989). Crabtree suggested that litter size is relatively insensitive to the level of exploitation.

Considering all of these findings, I would be inclined to reduce mean litter sizes slightly from the range of 4.5-9 pups/litter used in the C-L model to about 4-8 pups/litter in the revised model.

Natural mortality functions. The C-L model had 2 density-dependent natural mortality functions (Connolly and Longhurst 1975:Fig. 4). They assumed annual natural mortality of 40% for adults and approximately 61% for pups in an unexploited population. These rates declined to 10% as the coyote density was reduced to 0 by control kills. As with the birth functions, these mortality functions were conjectural, and there is little basis in new research to help refine them.

A review by Knowlton and Stoddart (1983) showed that annual adult mortality rates of 25-45% are common with 65-75% mortality indicated in a few studies. This report also drew attention to apparent high rates of post-natal losses of pups, perhaps as high as 30 to 60% during the first 6 months of life. Nellis and Keith (1976) estimated mortality rates (all causes) of 71% for pups and 36-42% for coyotes over 1 year old. Gese et al. (1989) found annual mortality rates for adults, yearlings, and pups of 13, 48, and 49%, respectively. These workers also reported that resident coyotes, transients, and dispersers had annual mortality rates of 13, 39, and 61%, respectively. The Gese et al. study took place on a 400-mi^2 area where coyotes were not exploited; however, coyotes were exploited on surrounding areas. The relatively unexploited population[2] studied by Crabtree (1989) was found to have annual adult mortality of only 10%, but 58% of pups died during their first 14 weeks of life. Crabtree suggested that early pup survival is the major reproductive response to exploitation.

Considering all these sources of information, I would be inclined to retain the C-L model's current natural mortality function for pups, where much of the annual mortality occurs in the first month or two after birth. I would replace the single adult mortality function in the C-L model with 3 functions--one for yearlings, another for 2-6 year adults, and another for older animals. Prime-age adults (i.e., 2-6 years old) would have lower mortality rates than yearlings or coyotes older than 6 years.

Immigration and emigration. The C-L model assumed that immigration and emigration either did not occur or occurred at equivalent rates. Connolly

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[2]Crabtree's study area in eastern Washington certainly supports 1 of the least exploited coyote populations in the lower 48 states, but all the adult coyote mortality he recorded was associated with human causes and there was a net loss of animals through egress. Thus this population should be regarded as lightly exploited, not unexploited.

and Longhurst (1975) agreed with Knowlton's (1972) contention that immigration (dispersal or infiltration) of coyotes from lightly hunted areas provides the mainspring for restocking areas under high rates of exploitation, but they left this aspect of coyote biology out of the C-L model because they couldn't devise a workable rationale to simulate it. Other coyote models reviewed by Connolly (1978) also omitted ingress and egress, perhaps for the same reason.

Biologists have made few advances on this topic over the past 20 years. Immigration has continued to be identified as a major element of coyote population dynamics (Connolly 1978; Knowlton and Stoddart 1983; Gese et al. 1989; Crabtree 1989). However, information on rates of ingress and egress and the explanations for these movements remain scanty (Knowlton and Stoddart 1983). More recently published coyote population simulations (Sterling et al. 1983; Windberg and Knowlton 1988) also failed to account for ingress and egress.

Perhaps one reason why modelers haven't made more effort to simulate the dynamics of unbounded coyote populations is the attractive simplicity of models involving closed populations. In real populations, coyote numbers change over time as the aggregate product of births, deaths, ingress and egress. But in a closed population, coyote numbers can change only through births and deaths, and recruitment to any age class consists of the survivors from a younger age class.

Given the relative simplicity of computing the dynamics of closed populations, some modelers could find it convenient to ignore immigration and emigration, even if workable techniques were available to simulate these processes.

It seems likely that someone eventually will devise a practical way to integrate ingress and egress in coyote simulation models. Pending such developments, the best way to minimize the adverse effects of ignoring ingress and egress may be to limit the application of coyote population models to large geographic areas, the larger the better. On small areas, I speculate that the erroneous assumption of a closed population, if substantial ingress actually occurs at high rates of exploitation, would yield model output that understates a coyote population's resilience to control.

Also, it seems that any errors introduced by assuming populations to be closed decrease in proportion to the size of the area occupied by the simulated population. That is, it may be invalid to assume that the population on a small geographic area is closed but more valid to make such an assumption for a large area. Of course, a population could in fact be closed if it inhabits an island or is bounded by large water bodies, coyote-proof fences, or other genuine barriers to coyote movements. Truly closed coyote populations, however, are extremely rare if they exist at all.

Computing hardware. The C-L model ran on a Wang Model 360 electronic calculator with a CP-1 card programming attachment. This calculator displayed results visually; there was no printed output. The program was designed with stop commands at each critical point so that, as computations proceeded, each desired result could be copied manually from the display.

As crude as this may seem by 1995 standards, it worked quite well in 1974. The slow computation speed was not a problem, but the Wang unit did not have enough memory to allow separate computations for animals by year classes. Also, it would have been desirable to compute births and deaths on monthly rather than annual cycles, but this would have been nearly impossible with the Wang system.

In 1995, of course, one would not run a simulation model on a programmable calculator but on a desktop computer using statistical software. Output would be printed and could include both tabular and graphical summaries. In my conception, the revised C-L model would run on a variety of computer models and be transportable on floppy discs or by electronic transfer.

One feature of the C-L model that could and should be retained in any update is its mathematical simplicity. The C-L model involved no computations other than simple addition and multiplication, and I know of no reason why an updated model should be more complicated.

Discussion

It appears to me that wildlife biologists' understanding of coyote population responses to exploitation have not changed appreciably over the past 20 years. Additional studies have refined the numerical ranges of some parameters, but the new

information confirms rather than revises the concepts set forth in Knowlton's (1972) landmark paper. Most coyote population simulations (including the C-L model) add little more than descriptive arithmetic to Knowlton's model, which elucidated the basics of coyote population mechanics in a form that has seen little improvement since 1972.

The C-L model was based largely on Knowlton's (1972) concepts and information. Except for revisions to incorporate the mechanisms of ingress and egress, which eluded Connolly and Longhurst (1975) as well as other coyote simulation models to date, I see no need for major revisions in the C-L model.

This is not to say that there have been no advances in our understanding of coyote population biology. Since 1972, Knowlton and others have identified social intolerances as an important factor in, if not the basis for, natural regulation of coyote population density (Knowlton and Stoddart 1983, Gese et al. 1989). The territorial pair is now recognized as the basic unit of coyote populations, and disruption of social patterns may be an important, undesirable result of exploitation (Knowlton 1989, Crabtree 1989). To date, however, these principles have not been applied to coyote simulation models.

Simulation efforts since 1975 have tended to confirm the C-L model in showing that coyote populations can support high rates of exploitation. Sterling et al. (1983) found in their simulations that control programs inflicting less than 50% annual mortality could not be expected to produce declining populations using any combination of litter size and percent breeding. Windberg and Knowlton (1988) showed that the number of coyotes actually using small geographic areas, and therefore the number that would have to be removed to gain population control, is much greater than one might infer from density estimates. Therefore, it appears that the main conclusions stated by Connolly and Longhurst (1975) remain valid today.

There have been major changes on the computing front, however. The programmable calculator used for the C-L model was scrapped long ago, and the utility of this model would be very much enhanced by revamping it to run on modern computers. Improved realism would result from incorporating the changes detailed earlier in this paper, but I expect that the updated model would generate results similar to those produced by the C-L model.

The updated model would be particularly useful to biologists who need a way to evaluate ADC programs or other human impacts on coyote populations in specific geographical areas, e.g. states, ecological regions, national forests, or BLM resource areas in connection with the preparation of environmental analyses under the National Environmental Policy Act.

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