

Comparison of discriminant function and classification tree analyses for age classification of marmots

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We evaluated the predictive power of two classification techniques, one parametric – discriminant function analysis (DFA) and the other non-parametric – classification and regression tree analysis (CART), in order to provide a non-subjective quantitative method of determining age class in Vancouver Island marmots (*Marmota vancouverensis*) and hoary marmots (*Marmota caligata*). For both techniques we used morphological measurements of known-age male and female marmots from two independent population studies to build and test predictive models of age class. Both techniques had high predictive power (69–86%) for both sexes and both species. Overall, the two methods performed identically with 81% correct classification. DFA was marginally better at discriminating among older more challenging age classes compared to CART. However, in our test samples, cases with missing values in any of the discriminant variables were deleted and hence unclassified by DFA, whereas CART used values from closely correlated variables to substitute for the missing values. Therefore, overall, CART performed better (CART 81% vs DFA 76%) because of its ability to classify incomplete cases. Correct classification rates were approximately 10% higher for hoary marmots than for Vancouver Island marmots, a result that could be attributed to different sets of morphological measurements. Zygomatic arch breadth measured in hoary marmots was the most important predictor of age class in both sexes using both classification techniques. We recommend that CART analysis be performed on data-sets with incomplete records and used as a variable screening tool prior to DFA on more complete data-sets.

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Knowing the precise age of an animal is critical for ecological studies of life-history theory or population dynamics. Changes in reproduction and survival with age form the foundation of life-history theory (Williams 1957, Roff 1992, Stearns 1992) and many population growth models (Oli and Dobson 1999, Schwarz and Seber 1999, Caswell 2001). Age-specific demographic rates are also essential for the development of conservation strategies for endangered species (Murphy and Noon 1992). Age has been determined from physical

characters with annual incremental growth (e.g. horns, Hik and Carey 2000; tooth cementum, Goodwin and Ballard 1985; otoliths, Horn and Sullivan 1996; mandibles, Millar and Zwickel 1972, Iason 1988) or from characters correlated with age (e.g. skeletal measurements, Zimmerman 1972; telomere restriction fragment length from DNA, Hausmann and Vleck 2002; tooth wear, Gipson et al. 2000). Without age indicators, age-specific parameters in an analysis must rely on a long-term record of individuals marked from birth (Lebreton

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et al. 1992). Calculating age-specific parameters for long-lived animals is especially important but challenging, and requires large sample sizes of individuals monitored for long-periods of time, often decades (Loery et al. 1987, Clutton-Brock et al. 1996, Schwartz et al. 1998, LeBlanc et al. 2001).

Even in an intensive mark-recapture study where every animal in the population is marked at first capture, knowing the age of all individuals is unlikely, unless the study continues beyond the life-span of the oldest animal and immigration of new animals is restricted to a single known age class. The ability to estimate the ages of unknown-aged animals in a data-set is particularly valuable for a number of reasons including increasing sample sizes to improve estimates of age-specific parameters, reducing study duration, and identifying age-specific immigration. This need is especially true for species with limited data because of high effort per capture or because they are rare or endangered. Determining relationships between age and physical characteristics can be challenging when there is variation in these variables or where there are interactions among variables because of allocation tradeoffs in mass, reproduction, or skeletal growth. Consequently, ecologists and wildlife managers require statistical techniques capable of detecting complex interactions among variables in small or incomplete data-sets in order to generate robust predictive models for age classification.

We compared two statistical classification techniques for predicting age of Vancouver Island marmots (*Marmota vancouverensis* Swarth) and hoary marmots (*M. caligata* Eschscholtz) that were not captured at birth in order to include more animals in calculations of age-specific parameters for building age-structured population models. We built and tested age classification models using one parametric and widely used technique in ecology, discriminant function analysis (DFA), and one non-parametric and relatively unfamiliar technique in ecology, classification and regression trees (CART: Breiman et al. 1984).

Study species

The Vancouver Island marmot is endemic to Vancouver Island, Canada (Banfield 1974, Nagorsen 1987) and is currently listed as endangered (Janz et al. 2000). As of September 2003, less than 110 individuals exist, with 78 in a captive breeding program, therefore the opportunity for collecting data for calculating age-specific demographic rates is limited. The sample size of known-age marmots from older age classes is small, therefore, to establish accurate age-specific demographic rates, it is necessary to extract as much information from the existing capture data by assigning ages to marmots without known ages.

The hoary marmot is closely related to the Vancouver Island marmot (Steppan et al. 1999), with a broad distribution throughout the mountainous regions of north-western North America from Washington and Montana to Alaska (Banfield 1974). The hoary marmot is genetically (Kruckenhauser et al. 1999, Steppan et al. 1999), behaviourally, ecologically, and physiologically similar to the Vancouver Island marmot (Barash 1989) and therefore provides the ideal opportunity to investigate ecological processes in healthy wild marmot populations which are relevant to the recovery of Vancouver Island marmots. We have three reasons for performing the age classification analysis on hoary marmots. First, comparing the two statistical techniques using two independent data-sets allows a more rigorous evaluation of the merits of each technique since different sets of variables were measured for the two species. Second, the hoary marmot data-set includes a larger sample of known-age class individuals and therefore allows us to evaluate the techniques despite the sample size limitations for Vancouver Island marmots. Third, assigning age-classes to unknown-age hoary marmots will allow us to determine more accurate age-specific demographic rates for hoary marmots for comparative population models between hoary and Vancouver Island marmots.

Marmots are large fossorial squirrels that spend more than half the year in hibernation during winter (Barash 1989). All growth, maintenance, and reproduction occurs within a four to six-month summer period before the onset of their next hibernation. Vancouver Island marmots and hoary marmots are reproductively mature at three years of age and are capable of producing only a single litter during the four-month active period (Barash 1989, Bryant 1996). Breeding by VIM at two years of age is rare (Bryant 1996, 1998). Juveniles appear above ground during mid season and therefore have less time to accumulate fat reserves sufficient for survival during hibernation than do adults. For simplicity, marmots are classified a year older immediately after each hibernation event although technically they are not a year older until later in the season. In preparation for winter hibernation, marmots exhibit tremendous seasonal changes in mass (30–50%) between spring and fall (Barash 1989). Therefore mass may overlap greatly among age classes. For example, a yearling marmot in spring may have a similar body measurement as it had late during the previous fall before hibernation when it was still a juvenile, however, it's mass will be 30% less. In marmots, morphological measurements may have complex interactions among each other and time of year in relation to age. Therefore marmots pose a considerable challenge for statistical techniques in age classification and therefore are ideal for evaluating the abilities of DFA and CART.

Methods

Classification techniques

Discriminant function analysis

Discriminant function analysis (DFA) is a commonly used parametric multivariate technique for classification in ecology (Williams 1983). DFA has been used to separate and classify community types (Saetersdal and Birks 1997), species (Green et al. 1996), behaviour (Boonstra 1984, Holekamp 1986), and habitat use (Karels and Boonstra 1999). Detailed descriptions on the use and applications of DFA can be found in many multivariate statistics textbooks (Manly 1991, Tabachnick and Fidell 1996), therefore we provide only a brief description of the use and assumptions of DFA. DFA is an extension of multiple regression analysis and multivariate analysis of variance (MANOVA: Tabachnick and Fidell 1996, McGarigal et al. 2000) in that it uses a linear combination of values (canonical functions) from two or more independent variables (discriminating variables) that best separate cases into their a priori assigned discrete classes in a dependent grouping variable. Multiple discriminant functions are sometimes required to reliably discriminate among classes when classes differ among many dimensions. The linear relationship among a set of discriminating variables that best separate the classes are represented by the first function. An orthogonal function to the first is found that next best separates the classes using a different association of discriminating variables. The number of functions is either equal to the number of discriminating variables or one less than the number of classes, but a reliable separation of classes is typically found with only the first two functions (Tabachnick and Fidell 1996).

Tabachnick and Fidell (1996) and McGarigal et al. (2000) describe in detail several assumptions and diagnostics that are associated with DFA: 1) homogeneity of variance-covariance matrices, such that the variance within each variable and the correlation among variables is similar among the groups. McGarigal et al. (2000) claim that equality of variance-covariance matrices is the most important assumption of DFA. 2) Discriminating variables have a multivariate normal distribution. 3) A discriminating variable must not be perfectly described by a linear combination of other variables (singularities). High correlations among discriminating variables (multicollinearity) warrants caution in the interpretation of functions (Williams 1983) but is not a specified assumption (McGarigal et al. 2000). 4) Random samples are drawn independently. 5) DFA is highly sensitive to outliers. 6) The probability of class membership for each case must be known prior to building the discriminant model. 7) Relationships among discriminating variables are linear.

Classification trees

Classification trees are a non-parametric binary recursive partitioning procedure developed by Breiman et al. (1984) as a means of assigning cases to two or more categories given a set of descriptor variables. The methodology, frequently referred to as CART (classification and regression trees), has been used extensively as a means for clinical risk assessments (Begg 1986, Steadman et al. 2000, Hulan 2001), however ecologists are just recently recognizing the strength of CART as a classification analysis tool (De'ath and Fabricius 2000, Vayssières et al. 2000). In ecology, CART has been used to classify physiological stages (Smith et al. 1997), species distributions (Vayssières et al. 2000), community distributions (De'ath and Fabricius 2000), and land-use changes affecting species abundance (Mankin 1999). In comparison with other statistical methods, CART analysis has been shown to perform equally or better than logistic regressions (Germanson et al. 1998, Rudolfer et al. 1999, Wietlisbach et al. 1999, Vayssières et al. 2000), discriminant function analysis (Smith et al. 1997, Kirkwood et al. 1989), and neural networks (Selker et al. 1995).

There are a number of advantages that CART analysis offers compared with traditional parametric multivariate techniques. Since classification trees are non-parametric (i.e. values are ranked), they do not assume any specific distribution of the data, and thus are not influenced by data transformation, nor are they influenced by outliers (Breiman et al. 1984, De'ath and Fabricius 2000, Vayssières et al. 2000). Parametric multivariate techniques require that missing values are replaced (e.g. with an average value) or that the entire case be deleted. For some data-sets, a number of missing values from one or more variables may render an analysis biased or unworkable (Breiman et al. 1984, De'ath and Fabricius 2000), however, in the construction of a classification tree, cases with missing values are assigned to a class using a surrogate variable. Surrogate variables are those variables that most closely agree with the original splitting variable and therefore act to gain the most information from the data-set (Breiman et al. 1984, De'ath and Fabricius 2000). Parametric multivariate techniques are also sensitive to strong correlations among explanatory variables (i.e. collinearity, Tabachnick and Fidell 1996) whereas collinear variables are identified as surrogates in CART and strengthen the analysis by maximizing the amount of available information (Breiman et al. 1984, De'ath and Fabricius 2000).

Vayssières et al. (2000) consider the use of "conditional information" as the most important advantage of CART analysis. In CART analysis, variables can be selected multiple times at each stage unlike in parametric stepwise procedures where a variable is included only once or not at all. CART considers all variables at each split regardless of whether they were used or not in the

previous split and thus chooses the variable that contains the most information in the multivariate space it is analyzing (Vayssières et al. 2000). The strength of CART is in determining complex interactions among explanatory variables. Such non-additive effects are often missed in linear additive models unless the interaction terms are specified a priori.

In CART, data are split at a parent node at a determined value along a range of values for a variable thus producing two child nodes with greater homogeneity (purity) than the parent node. Child nodes are recursively treated as parent nodes, thereby continuously splitting the data until a stopping criteria is reached and a set of terminal nodes are produced which in total resemble an inverted tree. Each terminal node is assigned a class that is determined by the class representation in that group. Breiman et al. (1984) identifies three elements that are central to the formation of a tree: 1. The selection of the splits; 2. Decision when to declare a node terminal or to keep splitting, and 3. The assignment of each terminal node to a class.

CART will split a node after considering all possible splits of cases (n) in each variable or linear combination of variables (k) thus producing a set of $n \times k$ possible splitting candidates. Each candidate split has a unique splitting rule that asks a question of the data that requires a binary answer (e.g. is body mass ≤ 500 g?). Each candidate split is ranked according to a measure of impurity (i.e. how well the classes are separated), which is also known as a “goodness of split” criterion (Breiman et al. 1984). De’ath and Fabricius (2000) describe three common criterion that are used to minimize the impurity of each node: 1. The “entropy index” minimizes within group diversity using the Shannon-Weiner diversity index. In early splits, this index tends to create nodes containing more than one class. 2. In contrast, the “Gini index” tends to split off the largest category into its own group. 3. The “twoing index” is normally used when there are ≥ 2 categories and separates data by grouping together multiple similar classes near the top of the tree index and isolating single classes at the bottom of the tree. It is optional for each of these splitting criteria for groups to be split on criterion using linear combinations of multiple variables when linear relationships among continuous variables exist (Steinberg and Colla 1997).

Trees are grown until nodes cannot be split further because there is only one case, or all cases belong to the same class, or the node has reached a predetermined size where splitting is halted. Ultimately, CART can create a tree that will completely describe the data at hand, and at extreme classification, each node can be occupied by a single case. However, as with stepwise linear regression procedures, adding variables will continuously increase the fit of the model to the data, but at the cost of increasing the true misclassification rate in an indepen-

dent data-set (i.e. no predictive power). Breiman et al. (1984) regard setting stopping rules as an inappropriate way of determining the right sized tree and recommend that trees be overgrown then “pruned” upward until reaching the tree with the lowest true misclassification rate. In ideal circumstances when sample sizes are large, data are split into two sets, a learning set and a test set where the best tree can be determined from its ability to accurately classify cases in the test set of data. However, for small sample sizes, alternative procedures have been developed that determine misclassification costs where data cannot be feasibly split into two groups.

The most popular method is “V-fold cross validation” which selects the best estimated predictive tree with the smallest estimated error. In V-fold cross validation, data are divided randomly into V approximately equal sized sub-sets, where V is usually 10. In turn, each sub-set is dropped out and a tree is constructed using the remaining 90% of the cases. The estimated error of the tree is then determined using the excluded sub-set as a test sample. This procedure is repeated for each of the 10 sub-sets and for every possible size of tree. The tree with the smallest estimated error rate is selected as the best tree, which is then grown using all of the data. Cross validation tends to produce a conservative estimate of tree size because trees used for testing are grown from a portion of the data. However, simulation exercises have shown that cross-validation estimates produce trees that are close to optimal tree size (Breiman et al. 1984).

After cross-validation, it is typical that there are several trees with error rates that are within ± 1 SE range of the tree with the minimum misclassification cost. Since the position of the minimum cost tree may be unstable from small changes in parameter values or even in the seed of the random number generator, Breiman et al. (1984) recommends that the smallest tree within 1 SE of the minimum tree be selected. This procedure results in a simpler tree that avoids problems of instability while providing a tree that is comparable in accuracy with the minimum cost tree.

Data collection

From 1987 to 2001, Vancouver Island marmots on Vancouver Island, British Columbia, Canada were live-captured in Havahart traps (Woodstream Corporation, Littitz, PA) baited with peanut butter. Marmots were released into a canvas cone bag and sedated with a mixture of Ketamine hydrochloride (Rogarsetic®, Rogers Pharmaceuticals, Vancouver, British Columbia) and Midazolam (Versed®, Hoffman-La Roche Ltd., Mississauga, Ontario) to facilitate identification of sex and measurement of morphological characters (Table 1) (Bryant 1998). At capture, marmots were assigned a known-age class or presumed-age class. Known-age

Table 1. Sample sizes of capture records with morphological measurements from known-aged Vancouver Island marmots and hoary marmots. The variables used for classification analysis are listed, however, body length and tail length for Vancouver Island marmots was not used for discriminant function analysis because they were components of total length but were used for classification tree analysis. Both species were classified to age class 4 (4 years of age or older). However, male Vancouver Island marmots ≥ 3 years were pooled into age class 3 before analysis owing to the small sample of 3-year-old males.

Age class	Vancouver Island marmot		Hoary marmot	
	Female	Male	Female	Male
0	57	59	50	78
1	35	26	70	110
2	8	10	69	71
3	8	2	23	20
4	30	14	140	31
	138	111	352	310
Total	249		662	
Variables measured				
	Julian day of capture		Julian day of capture	
	Weight		Weight	
	Total length		Total length	
	Body length		Zygomatic arch	
	Tail length			
	Forearm length			
	Hind foot length			
	Neck circumference			
	Chest circumference			

classes were assigned to marmots that were first captured as juveniles or yearlings. Presumed age classes were assigned for animals known to be alive for more than three years. Yearlings are easily distinguishable from juveniles and other marmots in that they are the only small dark marmot to appear before mid-June. Therefore, the following known age classes were used for Vancouver Island marmots: 0 (juveniles), 1 (yearlings), 2 (2-year olds), 3 (3-year olds), and 4 (≥ 4 -year olds). Of the 249 known-age marmot records we used in our analysis (Table 1), 50 records were from animals in captive breeding facilities. This was necessary in order to increase the sample size of older age animals, and adult marmots in captivity are morphologically indistinguishable from wild marmots (A. Bryant, unpubl.).

From 1999 to 2002, hoary marmots from the southwest Yukon (138°W, 62°N) were captured in tomahawk live-traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) baited with vegetation and urine (Holmes 1979). Handling of hoary marmots was similar to that for VIMs except that they were not sedated. Therefore some measurements recorded for Vancouver Island marmots were not recorded for hoary marmots (Table 1). Known-age hoary marmots consisted of those captured as juveniles or yearlings, or if the animal could be determined to be at least 4 years old in 2001 and 2002 (i.e. reproductively mature in 1999 or 2000 as determined by females with signs of lactation and males with

developed testis). Therefore, the same age classes were used for hoary marmots as for Vancouver Island marmots (i.e. 0–4). Except for male Vancouver Island marmots ≥ 3 years old, sample sizes in each age class (Table 1) for both species exceeded the recommended rule (McGarigal et al. 2000) of Williams and Titus (1988) where sample size must be equal to or greater than three times the number of discriminating variables.

Before analysis we separated males from females for both species owing to sexual dimorphism in marmots. We also randomly selected and put aside 15% of the data from each species and sex class separately to test classification rates of DFA and CART analysis.

Statistical procedures

Discriminant function analysis

We followed the procedures described by McGarigal et al. (2000) for testing the assumptions of DFA prior to analysis. All variables (Table 1) were used in the analysis except for the body length and tail length of Vancouver Island marmots because they are components of another variable, total length. For both species, all variables except date were log-transformed if necessary to improve normality and heterogeneity in distribution of data. This procedure improved most but not all distributions of age class-variable combinations. We deleted the most extreme outliers (beyond the 95th percentile) for each age-class variable combination. Although more outliers were detected after removing the first set of outliers, we did not delete these because of the impact of sample size reductions for some categories. Six (3 females, 3 male) outliers were deleted from the Vancouver Island marmot data and 14 (7 female, 7 male) were deleted from the hoary marmot data. We used Box's M-test as recommended by McGarigal et al. (2000) to test for equality of population covariance matrices. For both species and both sexes, covariance matrices departed significantly from equality. Therefore, DFA classification was conducted using group covariance matrices of the canonical discriminant functions as recommended by Tabachnick and Fidell (1996), and not those of the original variables. DFA was performed using a forward stepwise approach using a conservative probability of $P \leq 0.15$ for variable inclusion at each step as recommended by Costanza and Afifi (1979).

Classification trees

All CART procedures were performed using program CART 4.0 (Steinberg and Colla 1997) and performed using all variables (Table 1) of the same data that we used for DFA prior to deletion of outliers. Because CART is a non-parametric procedure, it was not necessary to examine data for outliers, normality,

heterogeneity, or any other multivariate assumptions as we did for DFA. We used the linear-combinations option for splitting groups owing to the linear structure of the data as recommended by Steinberg and Colla (1997). To improve the linear relationships among the hoary marmot variables we log-transformed all variables except Julian date as we did in the DFA. Linear relationships among the Vancouver Island marmot variables were not improved by logarithmic transformation and therefore untransformed data was used in the analysis. Splitting criterion was based on the Gini index, and we selected the smallest tree within 1 SE of the tree with the least classification error as determined using 10-fold cross-validation as recommended by Breiman et al. (1984).

Results

Discriminant function analysis

Prior to the DFA, cases with one or more missing values from discriminating variables were deleted (Vancouver Island marmot: males = 5, females = 7; hoary marmots: males = 20, females = 24). For both sexes of both species, the first discriminant function accounted for most of the variation (> 94%) and significantly discriminated among age classes, whereas a second discriminant function accounted for little variation (< 6%) and significantly discriminated age classes only in hoary marmots (Table 2). For female hoary marmots a third and fourth function were significant in discriminating between 2- and 3-year-old marmots but accounted for very little of the overall variation (0.5%).

Discriminating variables for age classes of Vancouver Island marmots differed between males and females (Table 3). Total length was important in discriminating age classes for both sexes, but multiple variables (weight, forearm length, hindfoot length and Julian day of capture) were included in discriminating age classes for females (Table 3). The similarity in pooled within-group

correlations for weight, forearm length, and total length for females suggests that these variables were correlated among themselves (Tabachnik and Fidell 1996). For hoary marmots, the zygomatic arch measurement ranked as the top discriminating variable for age class (Table 3) in both first and second significant discriminant functions (Table 2) and was therefore the most important variable in age class discrimination.

Plots of the canonical scores for the first two discriminant functions for both sexes of both species show the separation among age classes (Fig. 1). For male Vancouver Island marmots and male and female hoary marmots all age classes were significantly separated from one another (pairwise F-statistic comparison with $\alpha < 0.05$). For female Vancouver Island marmots, DFA could not significantly discriminate age-classes 2 and 3 from 4.

DFA correctly classified the age classes of 81% (n = 121) of the random marmot test data (Table 4). Classification rates in all cases were better than expected had age assignment been random. Classification rates between sexes were similar, although for Vancouver Island marmots, classification of older age classes (≥ 3 years) was better for females than for males. Classification rates were 10% higher for hoary marmots than for Vancouver Island marmots with greater than 72% correct classification for all age classes of both sexes.

CART

Our CART analysis of marmot age classes produced simple trees with terminal nodes separating all age classes (Fig. 2). The number of terminal nodes for each classification tree for both sexes of both marmot species was equal to the number of age classes in the data-sets indicating clear separation of the marmots into a single homogeneous group per age class.

For Vancouver Island marmots, the relative contribution of each variable as a primary splitting variable and

Table 2. Test of discriminant functions for age classification of male and female Vancouver Island marmots and hoary marmots.

Test of functions		% of variance	Wilk's lambda	χ^2	df	P
Vancouver Island marmots						
Males	1	98.5	0.19	138.6	6	< 0.001
	2	1.5	0.94	4.8	2	0.09
Females	1	97.6	0.18	179.0	20	< 0.001
	2	1.4	0.91	10.0	12	0.61
	3	0.6	0.96	4.3	6	0.63
	4	0.4	0.99	1.5	2	0.46
Hoary marmots						
Males	1	94.1	0.05	752.5	16	< 0.001
	2	5.6	0.59	133.8	9	< 0.001
	3	0.3	0.97	8.7	4	0.07
	4	0.0	1.0	0.1	1	0.74
Females	1	94.1	0.06	750.6	16	< 0.001
	2	5.5	0.62	126.9	9	< 0.001
	3	0.3	0.96	11.6	4	0.02
	4	0.2	0.99	4.0	1	0.04

Table 3. Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions coefficients describing age class in male and female Vancouver Island marmots and hoary marmots. Discriminating variables were selected by stepwise procedure entering only those variables that maximize the Mahalanobis distance between the two closest groups with a conservative minimum significance of F at $\alpha = 0.15$.

Variables in model		Function				Closest groups separated (* $\alpha < 0.05$, ** $\alpha < 0.01$)
		1	2	3	4	
Vancouver Island marmots						
Males	Total length	0.92	− 0.40	−	−	1,2**
	Neck	0.86	0.50	−	−	2,3**
Females	Weight	0.78	0.50	0.36	0.03	3,4*
	Forearm	0.78	0.15	− 0.06	0.16	3,4
	Total length	0.76	− 0.15	0.49	0.40	3,4*
	Hind foot	0.30	0.31	0.17	0.75	3,4**
	Julian day	− 0.19	0.24	0.79	− 0.54	3,4*
Hoary marmots						
Males	Zygomatic	0.62	0.65	0.32	0.12	2,3
	Total length	0.55	0.07	0.69	0.45	2,3**
	Weight	0.50	0.30	0.29	0.76	2,3**
	Julian day	− 0.15	0.40	0.51	0.75	2,3**
Females	Zygomatic	0.76	0.63	− 0.16	− 0.02	2,3*
	Weight	0.66	0.29	− 0.38	0.58	2,3**
	Total length	0.64	0.22	0.28	0.68	2,3**
	Julian day	− 0.09	0.54	− 0.31	0.78	2,3**

surrogate variable (when a primary splitting variable was missing for a case) differed between males and females (Table 5). The ranking of contribution scores for each variable differed whether their role as a surrogate splitter was considered or not. For male Vancouver Island marmots, forearm length contributed the most to age classification. Total length was an important variable in its total contribution, but chest circumference and weight contributed more as primary splitting variables when their role as surrogates was discounted. Hind foot length had no role in separating age classes, and surprisingly neither did Julian day, indicating that for males there are clear annual changes in morphology independent of seasonal changes in morphology. For female Vancouver Island marmots, splitting rules were more complex relative to splitting rules for males (Fig. 2). All variables played a role in the construction of the female tree although hind foot length had nominal contribution. Body length, weight, and total length had the greatest contribution scores. There tended to be more rules for each splitting criterion in the female tree compared with splitting criterion used for constructing the male tree showing that there were no single age-specific variables. Different age classes were associated with linear combinations of multiple variables with some variables, such as forearm length and chest circumference, appearing in multiple splitting criterion indicating interactions among variables in association with the age classes.

For hoary marmots the width of the zygomatic arch was the most important variable in determining age class for both sexes. The relative contributions of the other variables were ranked similarly for both sexes in the order of weight, total length, and Julian day of capture.

For both sexes there were complex interactions among variables used for splitting criteria (Fig. 2). For both males and females, day of capture and weight appeared in multiple splitting criteria indicating an interaction between the two variables in determining age class.

CART correctly classified the age classes of 81% ($n = 129$) of the random marmot data-set aside for testing (Table 4). Similar to DFA, classification rates for all age classes for both sexes of both species using CART were better than expected had age assignment been random. Classification rates between the sexes differed slightly but not consistently in both species. Classification rates were slightly better (6%) for male Vancouver Island marmots than female Vancouver Island marmots. Classification rates differed between the sexes of hoary marmots by only 2%. Age classification was 9–17% better for hoary marmots than for Vancouver Island marmots.

Discussion

Classification tree analysis performed no better or worse than discriminant function analysis in correctly assigning age classes to an independent data-set of known-age marmots. Both methods each correctly classified 81% of the marmots when both species were combined (Table 4). Neither method appeared to outperform the other when species or sexes were considered separately, although DFA appeared to be slightly better than CART at classifying older marmots than younger marmots (Table 4). For this reason, we might conclude that DFA is the marginally better method since morphological measurements asymptote with age making age

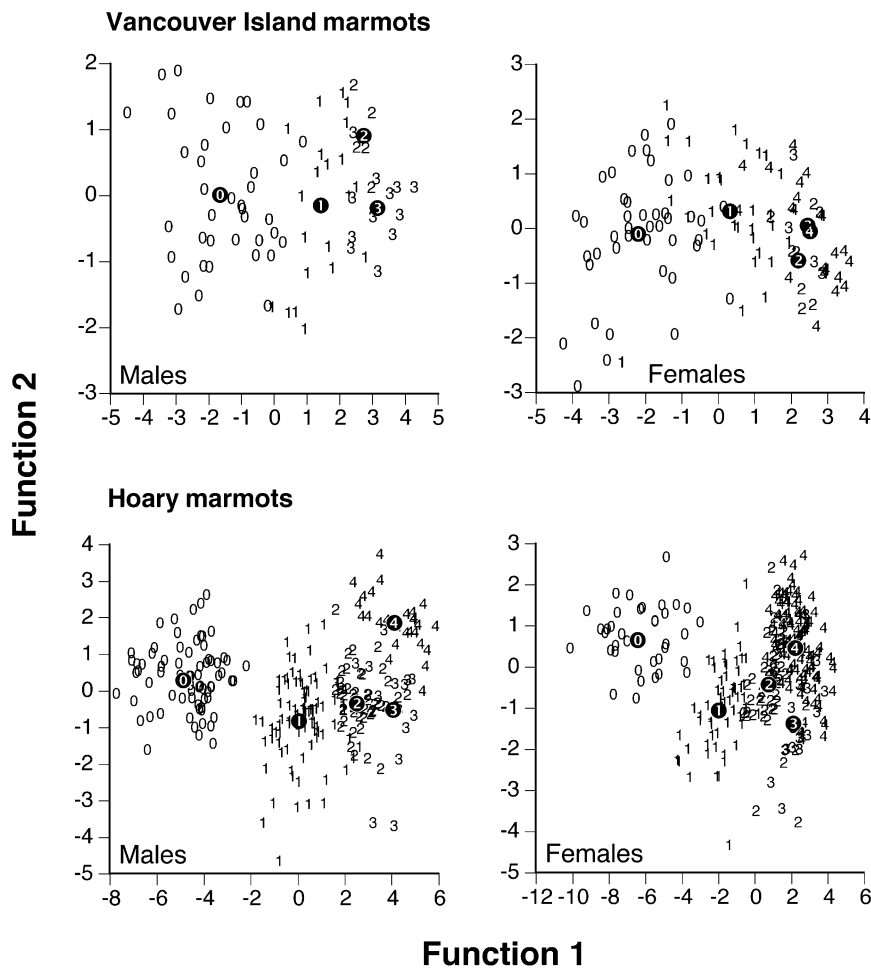


Fig. 1. Canonical scores for the first two discriminant functions derived from measurement and date variables describing the age classes of male and female Vancouver Island marmots and hoary marmots. Age classes are represented by numbers where juveniles are 0. Highlighted numbers represent the canonical score of the group centroid. The first discriminant function significantly separates the age classes of male and female marmots of both species (Table 2). The second discriminant function significantly separates the age of male and female hoary marmots only (Table 2). For both sexes of both species, age classes were significantly (pairwise F-statistic comparisons with $\alpha < 0.05$) separated from one another except for female Vancouver Island marmots where age classes 2 and 3 were not significantly separated from age class 4.

classification of older marmots the most challenging and the most useful. However, CART analysis may be a better tool for classification when we consider that DFA cannot assign classes to cases with missing values from the discriminating variables. In our marmot test samples, a total of eight cases were deleted by DFA thus reducing the true correct classification rate from 81% to 76% thereby making it a slightly poorer (5%) classification technique compared with CART analysis. One of the strongest advantages of CART analysis over DFA is its ability to substitute missing values in primary splitting variables with values from a closely correlated variable when making classification decisions (Breiman et al. 1984, De'ath and Fabricius 2000). Available data are more efficiently used by CART analysis than by DFA, and therefore we recommend CART analysis when analyzing incomplete data-sets.

The diagnosis of assumptions and the solutions for violations of assumptions of DFA require considerably more statistical skill when compared with CART analysis. Furthermore, ecological data rarely satisfy all the assump-

tions of DFA and therefore we must sometimes rely on the robustness of DFA to violations and/or interpret results with caution (McGarigal et al. 2000). We found that DFA performed admirably despite our violations of assumptions such as presence of outliers, non-normal distributions, unequal variance-covariance matrices, and multicollinearity. Meeting these assumptions in CART analysis is not required (Breiman et al. 1984).

Correct classification rates of age class were 9 to 11% greater for hoary marmots than for Vancouver Island marmots (Table 4). We attribute the difference in classification rates to the different sets of variables collected in our two independent field studies. The zygomatic arch breadth was the most important variable in discriminating ages for both male and female hoary marmots. Zygomatic arch breadth in Vancouver Island marmots has not been measured in the field but we expect that for that species, it may be as strong an indicator of age as it is for hoary marmots.

Variable importance was not consistent between the two classification techniques. For Vancouver Island

Table 4. Correct classification rates by discriminant function and classification tree analyses of age class in Vancouver Island marmots and hoary marmots. The same data was used to test the accuracy of the models derived by both techniques. The lower sample size in the discriminant function analysis is a result of the deletion of cases with missing values from discriminating variables.

		Age classes of random sample	Discriminant function analysis			Classification tree		
			Sample size	Expected (%)	Correct (%)	Sample size	Expected (%)	Correct (%)
Vancouver Island marmots								
Males	0	6	37	100	6	38	100	
	1	4	25	100	4	25	75	
	2	3	19	33	3	19	22	
	3	3	19	33	3	19	33	
	All	16	27	75	16	27	69	
Females	0	8	44	75	9	45	100	
	1	5	28	40	5	25	40	
	2	1	6	100	1	5	100	
	4	4	22	100	5	25	60	
	All	18	33	72	20	33	75	
Hoary marmots								
Males	0	5	15	100	5	14	100	
	1	15	44	80	16	43	75	
	2	7	21	86	9	24	100	
	3	4	12	75	4	11	75	
	4	3	9	100	3	8	100	
	All	34	28	85	37	28	86	
Females	0	10	19	100	10	18	100	
	1	11	21	82	11	20	100	
	2	10	19	80	10	18	83	
	3	4	8	100	5	9	60	
	4	18	34	72	18	32	72	
	All	53	24	83	56	19	84	
Total classification rates		121	27	81	129	25	81	

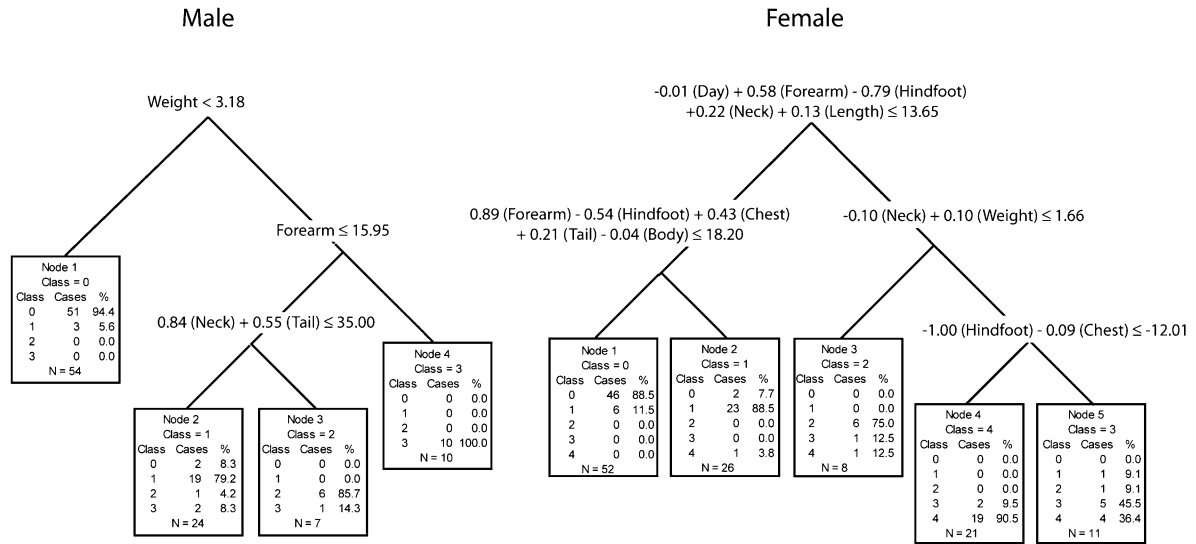
marmots, different variables were ranked as more important by DFA (Table 3 first discriminant function) than they were for CART analysis (Table 5). DFA and CART analysis were not in agreement in the selection and ranking of variables in discriminating age classes for Vancouver Island marmots. For example, for males, total length and neck circumference were the only two variables selected by DFA, whereas many variables (Table 5) were ranked by CART as having high relative contributions to splitting criteria. CART analysis did agree with DFA in that both total length and neck circumference were important variables in age classification. Similarly, for females, CART analysis agreed that weight, forearm length and total length were important. In classifying ages of hoary marmots, there was strong agreement between DFA and CART analysis in the selection of variables and their relative importance in age classification. The variables chosen and their ranking in importance (i.e. ranked zygomatic arch, weight, total length, and Julian day) were very similar for both sexes and both classification techniques.

Although model interpretation from CART analysis is simple compared with interpretation of DFA models (De'ath and Fabricius 2000, Vayssières et al. 2000), CART has been criticized by Grahl-Nielsen (1999) for its lack of information about relationships among classes, especially when the same class appears in different terminal nodes on different branches of the tree. Since

our objective was not in the interpretation of the relationships among variables but rather in the predictive power of CART, this not a concern. We agree with others (Crichton et al. 1997, Vayssières et al. 2000) that CART analysis prior to DFA may serve as an efficient method of screening data for important variables and detecting complex interactions among variables prior to conducting parametric analyses even if correct classification rates by CART are disappointing.

In conclusion, both DFA and CART analysis have excellent predictive power for determining age class in marmots. DFA still performed strongly despite the violations of its assumptions in our data-sets. We cannot conclude that one method is better than the other since judgment of these classification methods depends on two conditions, the completeness of the data and the objectives of the study. Our results showed that DFA was slightly better than CART at classifying older age classes although poorer at classifying younger age classes. Since our objective is to assign age classes to those marmots which are the most challenging to discriminate (i.e. the older age classes), DFA is the more appropriate method. However, since a number of our cases had missing values for some of the discriminant variables, CART performed slightly better overall since DFA could not classify cases with missing values. Therefore, CART analysis is a suitable alternative to DFA for incomplete data-sets. CART analysis in combi-

Vancouver Island marmots



Hoary marmots

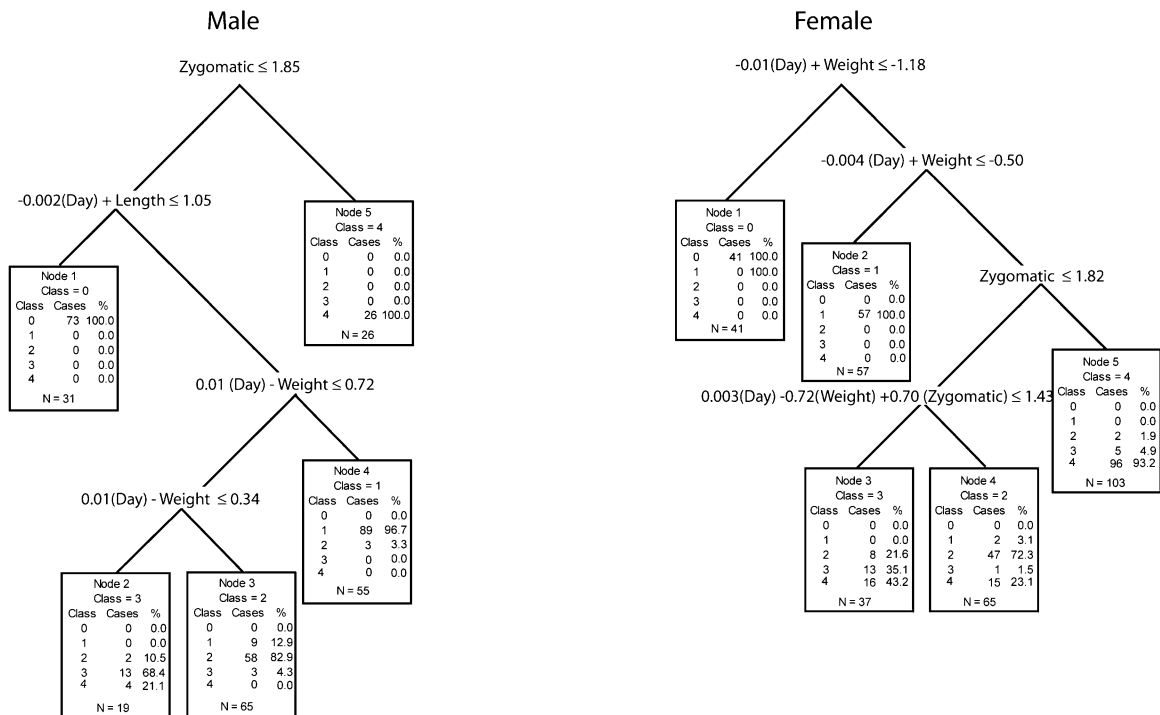


Fig. 2. Classification trees describing age class of male and female Vancouver Island marmots and hoary marmots. Splitting of each node was determined by a linear combination of variables where cases that meet the criteria at each junction are split off to the left. Trees shown are the smallest trees within 1 SE of the relative cost (mis-classification rate) of the smallest tree determined by 10-fold cross-validation. Each terminal node was assigned an age class according to the distribution of age classes that fell into the node. For both sexes of both species, the number of terminal nodes was equal to the number of age-classes assigned to the data.

Table 5. Relative ranking of variable contribution in splitting criteria for classifying age of Vancouver Island marmots and hoary marmots. Scores include 1) total contribution score — the relative contribution of a variable as a primary and surrogate variable in the splitting criteria at all nodes in the tree (Fig. 2 for classification tree) and 2) contribution score with surrogates discounted — the relative contribution of a variable discounted by its association with primary splitting variables as a surrogate variable.

Vancouver Island marmots					
Males			Females		
Variable	Contribution score		Variable	Contribution score	
	Total	Surrogates discounted		Total	Surrogates discounted
Forearm length	100.0	100.0	Body length	100.0	95.1
Total length	90.0	66.1	Weight	97.4	100.0
Chest circumference	89.3	74.8	Total length	85.8	93.7
Weight	79.2	75.5	Neck circumference	75.7	72.8
Body length	74.3	49.0	Forearm length	56.2	52.8
Neck circumference	71.7	65.5	Chest circumference	32.9	34.7
Tail length	8.6	3.7	Julian day	25.2	19.3
Hind foot length	0.0	0.0	Tail length	10.0	8.0
Julian day	0.0	0.0	Hind foot length	6.8	6.6
Hoary marmots					
Males			Females		
Variable	Contribution score		Variable	Contribution score	
	Total	Surrogates discounted		Total	Surrogates discounted
Zygomatic arch	100.0	100.0	Zygomatic arch	100.0	100.0
Weight	73.1	58.2	Weight	91.3	73.8
Total length	51.9	42.6	Total length	84.0	57.1
Julian day	9.1	3.6	Julian day	11.3	2.6

nation with DFA can be a very powerful approach for classification analysis for two reasons. First, CART analysis can be used as a quantitative method for screening for candidate variables and complex interactions among variables prior to parametric analysis. Second, cases can be classified according to the strengths of each method. In our analysis, DFA was slightly better at classifying older age classes while CART was slightly better at classifying younger age classes. We have also demonstrated that the choice of variables measured may have a strong impact on the success of age classification regardless of the statistical technique used. The best discriminating variables will differ among species and determining such may be challenging. Determining the variables that are closely associated with age early in a research program will be beneficial even if age-structure is not immediately important to the investigator. Long-term records of known-age individuals in populations are rare, but knowledge of age is crucial for studies of life-history evolution, population dynamics and the management and conservation of wildlife.

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