

**Glacial cycles promote greater dispersal, which can help explain
larger clutch sizes, in north temperate birds**

David W. Winkler^{1,4}

Russell Greenberg²

Thomas E. Martin³

Frederick R. Adler⁴

Samuel M. Flaxman⁵

¹Cornell University Museum of Vertebrates and Department of Ecology and
Evolutionary Biology, Ithaca, NY 14853

²Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C.
20008

³Montana Cooperative Wildlife Research Unit, University of Montana, Missoula,
MT 59812

⁴Departments of Mathematics and Biology, University of Utah, Salt Lake City,
UT 84112

⁵Department of Ecology and Evolutionary Biology, Princeton University,
Princeton, NJ 08544-1003

⁶To whom all correspondence should be sent: dww4@cornell.edu, FAX 607 255-
8088, Phone 607 254-4216

Abstract

Earth's glacial history and patterns in the life history traits of the planet's avifauna suggest the following interpretations of how recent geological history has affected these key characteristics of the biota: 1) Increased colonizing ability has been an important advantage of increased dispersal, and life history strategies are better categorized by dispersive colonizing ability than by their intrinsic growth rates; 2) Birds of the North Temperate Zone show a greater tendency to disperse, and they disperse farther, than tropical or south temperate birds; 3) Habitat changes associated with glacial advance and retreat selected for high dispersal ability, particularly in the North; and 4) Selection for greater dispersal throughout the unstable Pleistocene has also resulted in other well-recognized life history contrasts, especially larger clutch sizes in birds of North Temperate areas.

Introduction

Life history traits are those traits that most directly influence survival and reproduction, and avian patterns of life history variation have been influential in the development of life history theory (Charnov and Krebs, 1974; Lack, 1947; Lack, 1954; Lack, 1968; Stearns, 1992). One of the most long-standing and controversial patterns of variation has been the difference in clutch sizes between temperate and tropical birds (Boehning-Gaese, 2000; Godfray et al., 1991; Lack, 1947; Martin et al., 2000; Ricklefs, 1980; Skutch, 1949): birds in the north lay larger clutches than do those in the tropics, and current explanations for latitudinal variation in avian clutch sizes have relied on associations with present-day environments in these regions (Martin, 2004; Ricklefs, 2000; Ricklefs and Wikelski, 2002).

It is growing increasingly apparent that the clutch sizes of birds in the south temperate are often at least as similar to those in the tropics as they are to clutches at similar latitudes in the north (Martin, 1996; Martin et al., 2000; Rowley and Russell, 1991). Thus, what has been thought of as a gradient may actually be a major disjuncture, where north temperate clutch sizes are largely different from those in the rest of the world. Explanations for life history variation must be able to explain this major regional disjuncture in clutch sizes. Furthermore, given recent research on the likely role of Pleistocene events in shaping the genetic structure of populations (Avisé and Walker, 1998; Ball et al., 1988; Mila et al., 2000; Perez-Tris et al., 2004; Pianka, 1974), current theories of life history evolution are remarkably ahistorical.

In this paper, we develop a different perspective that derives from patterns of dispersal rather than clutch size. Dispersal is the organismal trait most directly involved in the expansions of ranges and the colonization of new habitats, and it is the one life history trait that demands explicitly spatial consideration. By considering the implications of recent geological history for the dynamic distributions of bird populations in different parts of the globe, we develop the hypothesis that regional differences in avian life history strategies are related to historical selection on dispersal strategies. In particular, we hypothesize that the expansion and contraction of glaciers caused by Pleistocene climate cycles, and the resulting loss and recovery of vegetation at the level of whole biomes, exerted strong selection on the life history strategies of birds occupying those biomes. In a future version of this manuscript, we will show with a simple model and simulation that this effect is real. We do not wish to suggest that these ideas are exclusive of hypotheses that link life history traits with current environments. Yet a comprehensive understanding of current patterns of life history variation may require consideration of selection resulting from large-scale changes in environments over the past few million years. Such considerations may provide a significantly improved understanding of global patterns in clutch size and other avian life history traits.

Glaciation, Dispersal and Biogeography

The last two and a half million years on Earth has been characterized by periods of advance and retreat of glaciers (Fig. 1). Climatic and ecological stasis has been rare and transitory. The dynamics of habitat availability differ between phases of glaciation (Fig. 2), but in both cases, long-distance dispersal may have been favored by selection—we are exploring these possibilities with modeling work in progress. If we for a moment

consider only the most recent glacial retreat, two factors must have selected for long-distance dispersal in northern birds: the retreat was followed by rapidly changing and expanding plant assemblages (Davis and Shaw, 2001) which constituted new opportunities for colonization (see Fig. 2 for graphical model). In the Northern Hemisphere, the rate of this habitat expansion increased with higher latitude because land area grows larger with latitude in both North America and Eurasia. In contrast, the Southern Hemisphere has decreasing land areas with higher latitude, increasing the marine influence on climate, reducing temperature fluctuations, ice coverage (Hubbard et al., 2005) and, hence, rates of habitat change further south.

Greater dispersal would also be favored in the North when glaciers advanced, but for different reasons. As climate cooled and glaciers expanded, local conditions deteriorated and birds had to move to track a southwardly receding front of habitat before it was colonized by a large pool of potential competitors. Again, because of the distribution of land-mass with latitude, these dynamic changes in temperature and habitats were most strongly expressed in north temperate zones. We, therefore suggest that North Temperate Zone birds represent a subset of species for which long-distance dispersal was more strongly favored than in more southern regions (i.e., tropics and southern hemisphere). Simultaneously, selection for long-distance dispersal favored an alternative suite of life history traits, such as production of more young with less investment per young, which typifies most north temperate bird species.

To support this heuristic model of the evolution of colonizing ability and how this would shape avian life history in the North Temperate Zone we will elaborate on the following four points: 1) Colonizing ability has been an important advantage of

increased dispersal and this advantage has molded patterns of dispersal; 2) Birds of the North Temperate Zone show a greater tendency to disperse, and they disperse farther, than tropical or south temperate birds; 3) Glacial advance and retreat and its associated habitat changes selected for high dispersal ability, particularly in the North; and 4) Selection for greater dispersal throughout the unstable Pleistocene has led to greater clutch sizes in birds of North Temperate areas.

1) Colonizing Ability, Dispersal and Life History Strategies

MacArthur and Wilson (1967) related ecological process to biogeographic pattern through their theory of *r*- and *K*-selection. By this view of life history (Pianka, 1974; Stearns, 1992), *r*-strategists produced many offspring with little per capita investment enabling them to rapidly reproduce in new environments. By contrast, *K*-strategists invested in fewer but larger young, which had greater competitive ability in already crowded environments. The *r*-*K* dichotomy dealt with the demographic ability of colonizing populations to thrive in their new habitats, not on the process of dispersal in the first place. The selection pressures and costs and benefits of dispersive movements *per se* were never part of the explicit theory of *r*-*K* strategies, and the *r*-*K* dichotomy was spatially static as a result.

Dispersal can be favored as a habitat becomes more crowded either from population growth (Myers and Krebs, 1971) or shrinking habitat size/suitability, both of which can increase mortality and decrease reproductive success. At the same time, the benefits of dispersal and, hence, selection favoring dispersal, increases with probability of encountering unoccupied or sparsely occupied habitat of high quality. This probability increases with size of the unoccupied habitat. Dispersal itself incurs costs from increased

mortality and/or probability of not finding suitable habitat for reproduction (Clobert et al., 2001). Thus, dispersal should be favored when the benefits, in terms of increased reproductive success from colonizing new habitat, exceed the costs (probability of mortality from dispersal *or* increased probability of not finding suitable habitat to reproduce *or* decrease in reproductive success or survival in non-natal habitat). These conditions are particularly well met by glaciation events, which yielded increased areas of unoccupied habitat during glacial retraction and increased crowding and shifting availability of suitable habitat during glacial advances (Dynesius and Jansson, 2000).

Advantages of dispersal and colonization of new habitats can be increased by production of more propagules. Clearly, having more offspring that disperse over greater areas would increase the probability of successful colonization just as would having large numbers of competing offspring at any site discovered (Harper, 1977). Thus, there is every reason to expect that birds that produce more dispersing young would be good at both discovering new habitats and competing in the early phases of colonization.

The critical characteristic of the colonizing strategy, however, is not its intrinsic population growth rate, but its dispersive ability, and we suggest that colonizing life-styles were favored in the North by long-term climatic instability and that they now characterize North Temperate birds to a degree not heretofore appreciated.

2) Dispersal in North Temperate species versus those elsewhere

Selection on dispersal may have played a larger role in the evolution of regional differences in life history traits (such as clutch and egg size) than is generally recognized. Dispersal is one of the most important life history traits to avian evolution and ecology (Clobert et al., 2001; Greenwood and Harvey, 1982). Yet, dispersal probably has not

received the attention it deserves because the pattern of dispersal distances (Baker et al., 1995; Koenig et al., 1996; Thomson et al., 2003) and its fitness consequences remain the most difficult of life history attributes to quantify.

Despite a paucity of data, it seems clear from a few large-scale studies and genetic estimates that the average dispersal distances of temperate zone birds can be at least several kilometers (Winkler, 2005; Winkler et al., 2005). Studies of dispersal distances in tropical birds are even rarer than for temperate species. The few population studies and estimates based on genetic analyses suggest, however, that at least in birds in forest in the tropics (cf. Brawn et al., 1996), mean dispersal distances of many species are short, with a high proportion of individuals settling within a few hundred meters of their natal territory (Bates, 2000; Capparella, 1992; Greenberg and Gradwohl, 1997; Joseph, 2005; Winkler, 2005). The dispersal distances of well-studied north temperate birds have another property that appears to set them apart from those of tropical birds: their distributions display a very long tail of a very few individuals dispersing very long distances (Hosner and Winkler, 2007), and it is these very long-distance dispersers that are likely to have enormous impacts on range changes (Veit, 2000; Veit and Lewis, 1996).

Measurements of the fitness consequences of variation in dispersal distance have proven inconclusive: birds that disperse longer distances can experience both higher (Altwegg et al., 2000) and lower (Pärt, 1991) subsequent success. The largest problem with these measures, however, is that they can be applied only to those birds that disperse successfully and establish themselves in a breeding population; the number of “losers” (i.e., those that die or fail to find a suitable territory to breed) in the effort to disperse a

long distance has never been assessed. Yet the ultimate cost of long-distance dispersal will be measured in the proportion of birds employing this strategy that never establish themselves and reproduce. This cost is likely to be generally high, not because of physiological constraints (most birds are capable of traversing the additional distances), but because of the uncertainty and mortality risks associated with exploring new habitats. To offset these costs, the benefits would have to compensate by providing more than just an opportunity for the dispersing individual to reproduce, but to provide greater sustained chances of competitor-free habitat for the disperser and its descendents. The pay-off for long-distance dispersal comes when the opportunities for dispersers shift from being local and short-term to becoming a strategy for sustained colonization of a moving frontier.

3) Historical Conditions Favoring Colonizing Ability in Northern Biota

Terrestrial landscapes on Earth have been through a remarkable series of rapid transitions over the past several million years. Much of the Northern Hemisphere has been intermittently under ice several thousand meters thick through a series of over twenty advances and retreats of continental glaciers. Periods of stasis have been short, with most of the geological record being marked by periods of growing or shrinking glaciers (Fig. 1). During the last glacial maximum, only 18,000 years ago, most of the temperate landscape of North America and Eurasia was covered by thick ice sheets (Fig. 3), or steppe, tundra or refugial woodland vegetation very different than occurs there today (Jackson et al., 2000; Willis et al., 2000). Thus, we can assume that the surviving north temperate avifauna, especially that occupying deciduous forest, is comprised of accomplished dispersers.

It is likely that most bird species in the Northern Hemisphere are living in places and environments that did not exist a relatively small number of generations ago. This recent history must be relevant to the preponderance of dispersers in northern faunas. That colonization of these habitats must have been swift and/or gene flow from dispersal remains high finds firm support in the recent findings of relative genetic homogeneity in north temperate bird populations (Joseph, 2005; Klicka and Zink, 1999; Lovette, 2005; Mila et al., 2000; Weir and Schluter, 2004; Zink et al., 2004). In short, the repeated alternation between glacial retreat and expansion that characterized the Pleistocene could have strongly favored dispersing genotypes/clades that still predominate in northern avifaunas today.

In highlighting the environmental changes in the North, we do not wish to suggest that environmental changes were not extreme elsewhere. Habitats throughout the globe were altered dramatically in the Pleistocene, with a general restriction, especially, of forested habitats throughout (for a discussion of the extent of refugia, especially in Amazonia, see (Carneiro et al., 2002; Colinvaux et al., 2000; Haffer and Prance, 2001; Willis and Whittaker, 2000). The North, however, was distinctive in the greater extent of land that was totally uninhabitable (under ice) and the great distances that birds occupying biomes with trees (and the trees themselves) needed to cover to re-establish forest communities in the North. Approximately 40% of the North American continent was covered by ice compared to less than 10% of South America (Fig. 3). The South American glaciers expanded, but remained within the Andean region or on the fringe of the Patagonian plains; forest, grasslands, and thornscrub shifted in distribution and relative importance, but without the extreme contractions found in North Temperate

regions (Clapperton, 1993). In addition, the latitudinal distribution of landmass in the Southern Hemisphere is the opposite of the northern pattern, which means that the available land decreased as birds colonized further south, and southern hemisphere climates were less severe than those in the north during glacial maxima (Hubbard et al., 2005). Birds in the Southern Hemisphere (and in parts of the mountainous North) were likely faced with reduced selection for dispersal, with most movement being shorter distance up-slope and down-slope rather than long distance north-south movements.

Once adjustments in fecundity are made to compensate for large losses in dispersal, selective pressures to return to a low dispersal life history may be extremely small. A careful balancing of the costs and benefits for dispersal distance in current environments may help explain why long-distance dispersal is still favored or why it has been slow to be down-tuned from historical levels. Indeed, some have suggested (O'Connor, 1985; Paradis et al., 1998) that northern habitats today present a mosaic of changing ecological opportunities that select for continued dispersal, the most dynamic of which are occupied preferentially by migrants. The dynamics of this mosaic is patchy, with some areas of habitat winking in and out in a repetitive way and others changing in a more directed way, as suggested by the recent steady movement northward of some southern forms (Parmesan and Yohe, 2003; Thomas and Lennon, 1999). The much larger land masses and greater extent of similar habitat available to birds in higher latitudes in the Northern Hemisphere may continue to provide persistent dispersal opportunities and lower costs (i.e., lower likelihood of arriving in an area of unsuitable habitat when dispersing far) at greater scales than further south. However, even in equilibrial environments, with only demographic stochasticity in the availability of habitat and a

persistent selection to avoid inbreeding and competition with kin, dispersal in a surprising proportion of offspring, and over surprisingly large distances, can be favored (Comins et al., 1980; Greenwood-Lee and Taylor, 2001; Hovestadt et al., 2001; Murrell et al., 2002; Ronce et al., 2000).

There is plenty of evidence for on-going dynamism, both anthropogenic and not, in the environments of the Northern Hemisphere, but the time since glaciation has been short, and a convincing understanding of the life histories of northern birds today must include the recency of origin of the environments they now occupy.

4) Selection for greater dispersal may account for larger clutches in northern regions

Returning to the broader issue of life history evolution, one of the most persistent patterns in the life histories of birds is the larger clutch sizes of birds in the North compared to closely related species in the tropics and further south (Klomp, 1970; Lack, 1968). We argue that organisms can respond to circumstances where long-distance dispersal is favored by investing in a greater number of dispersing young. Given the homoeothermic nature of birds and their generally exceptional powers of movement and sensory processing, there is no need to evolve a dramatically different dispersive phenotype, as in insects (Simmons and Thomas, 2004). Increasing the number of dispersing offspring is likely a very effective means of increasing the chances of colonization of both near and distant habitats that are vacant or sparsely populated. The extensive areas of similar habitats in north temperate regions decrease the cost of dispersal arising from reduced likelihood of finding suitable habitat from long-distance dispersal. Consequently, selection against high levels of dispersal and the high fecundity

that enables it may be weak. High levels of dispersal in the North, so strongly favored during periods of glacial advance and retreat, are likely easily maintained even in less rapidly changing times.

If higher fecundity is a necessary correlate of greater dispersal tendencies, then the greater clutch sizes in the North can be seen as an adaptation to dispersal and a consequence of the greater dispersion and accelerated range dynamics that it allowed historically and continues to support today. We thus add selection on colonizing ability for North Temperate Zone birds as another important factor that might explain the broad disjuncture in clutch sizes generally observed.

Conclusions: Dispersal, the link between global history and life history

Dispersal and its costs deserve a much closer look as a possible missing link between life histories and biogeography. Dispersal is clearly the way that ranges change, and it would be surprising if range expansion did not carry a survival cost for dispersing young that needed to be compensated by higher fecundity. Only those birds having the ability to rapidly expand their ranges northward and retreat southward have been able to track the rapidly changing distributions of habitats in the North that the Pleistocene has, for over two million years, created. Organisms able to meet this spatial challenge are necessarily different in their life histories than those that achieved persistence through other adaptive paths. The life histories of north temperate biota likely include other ghosts of colonizations past.

Testing the line of thinking presented here calls for integrating information from several areas and highlights the following needs for further research: 1) Measurement of patterns of natal dispersal from a much greater range of birds and other taxa inhabiting

habitats and realms that experienced different glacial histories; 2) Gathering more data on the historical dynamics of habitats in different regions, especially in the New and Old World tropics; 3) Further exploration of spatially explicit theoretical explorations of the effects of selection on life histories in landscapes with considerable periodic spatial and temporal dynamics; 4) Gathering detailed information on whether patterns of natal dispersal within species correlate with the history of habitat expansion (cf. (Perez-Tris and Telleria, 2002); 4) Development of methods to study the costs and benefits of different dispersal tendencies that include those individuals that fail to successfully disperse.

ACKNOWLEDGEMENTS

We thank M. Bursik, G. Huber, M. Kaplan, A. McCune, J. Mandel, P. Marks, and R. Safran for helpful comments during the gestation of these ideas. DWW's research was supported by a Cooperative Agreement with the National Center for Environmental Assessment, EPA (CR 829374010) and an NSF LTREB grant (IBN-013437).

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Figure 1. An overview of the last quarter million years of glacial history on Earth after <http://www.homepage.montana.edu/~geol445/hyperglac/time1/time.htm> and (Wright, 1989). Letters at the bottom correspond to the periods of glacial advance and retreat characterized by the panels in Fig.2.

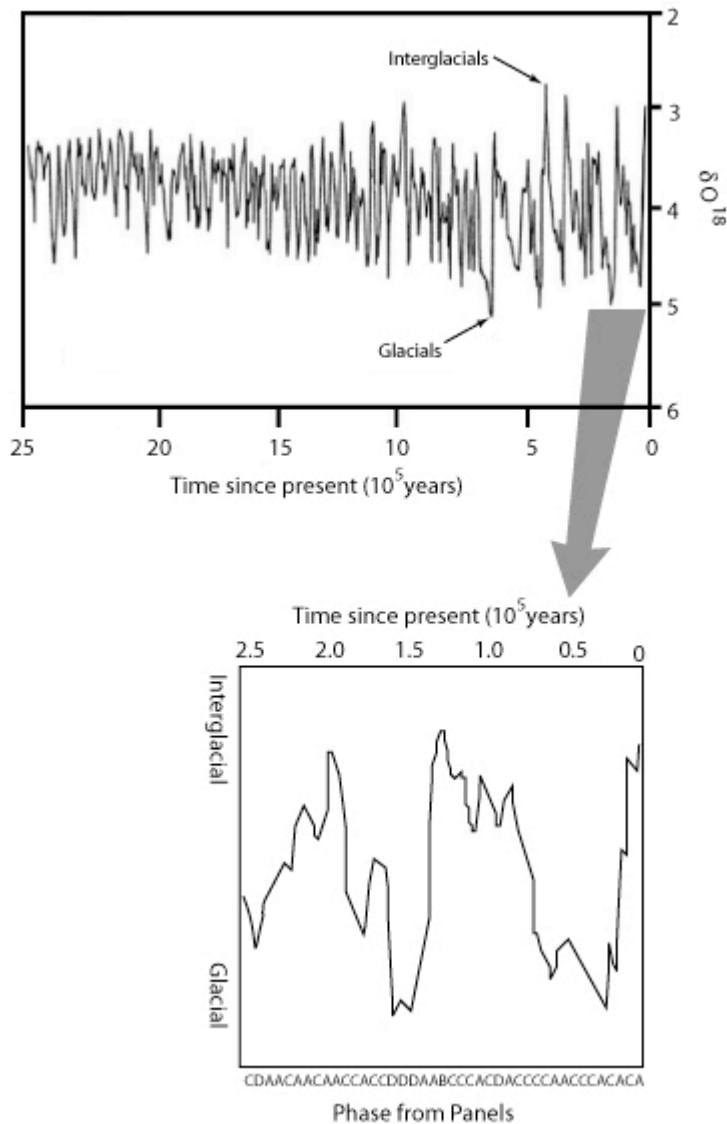


Figure 2. Simplified reconstruction of the dynamics of available (open circles) and filled (closed circles) habitat patches attendant on the retreats and advances (shaded arrows) of continental and mountain glaciers. As the ice recedes (Panel A), large quantities of unoccupied habitat appear. As the time and distance from the ice front increases (B), dispersive colonization occupies many habitat patches, and successional changes both in front of and behind the band of habitat can cause the appearance and disappearance of potentially colonizable habitat. Successional changes can continue to deplete the supply of available breeding sites, and when the ice begins to re-advance (C), the ice begins to limit site availability further in at least one direction. Late in glacial advance (D), breeding habitat availability is at its lowest. At all stages, the same template of dispersal distances (dotted arrows) is superimposed emanating from one habitat patch to show that, at times of habitat scarcity or high occupation rates, at least some long-distance dispersal is still favored, though at no stage is the availability of opportunities as great as during Early Glacial Retreat.

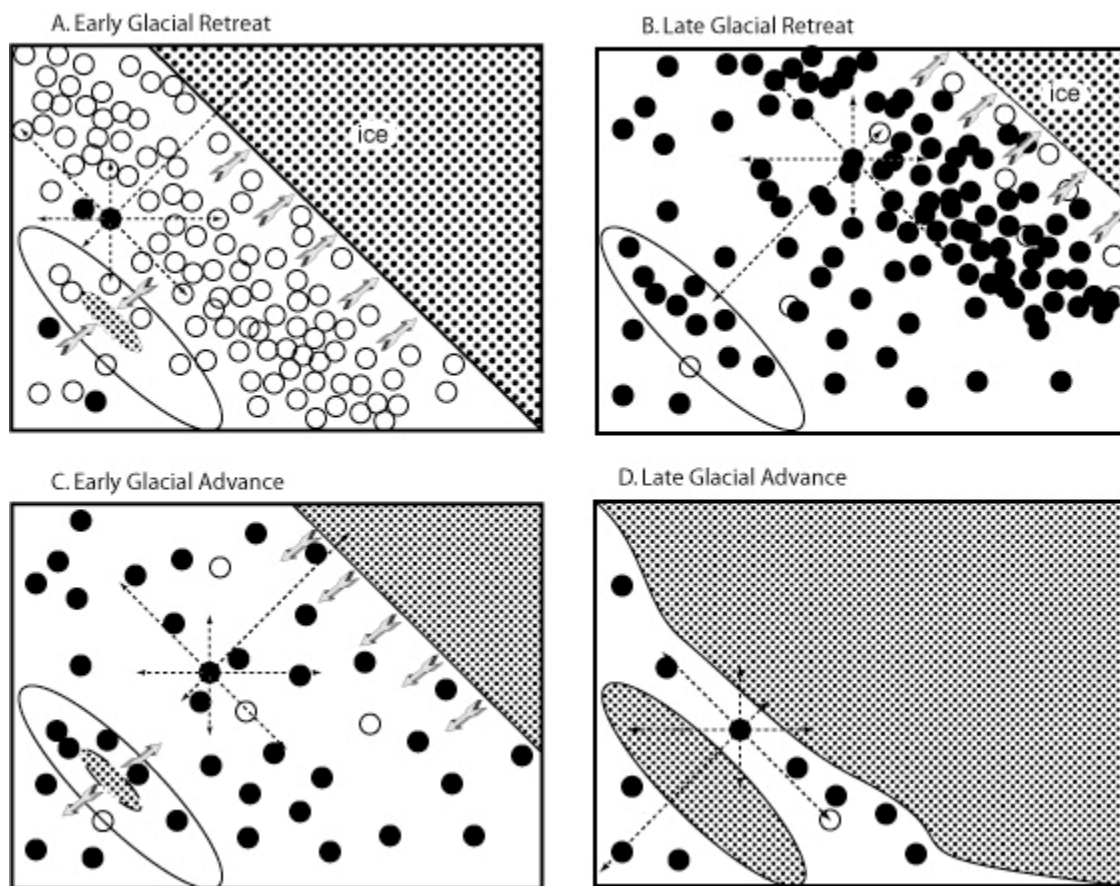


Figure 3. Approximate extent of ice (in black) during the Last Glacial Maximum 18,000 years ago, after (Denton and Hughes, 1981). Glaciologists currently disagree on whether ice cover in eastern Eurasia was during the LGM or an earlier Pleistocene event, but the extent of ice depicted still serves for the arguments in the present paper.

