
Applying Metapopulation Theory to Conservation of Migratory Birds

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Abstract: *Metapopulation theory has proven useful for understanding the population structure and dynamics of many species of conservation concern. The metapopulation concept has been applied almost exclusively to nonmigratory species, however, for which subpopulation demographic independence—a requirement for a classically defined metapopulation—is explicitly related to geographic distribution and dispersal probabilities. Defining the degree of demographic independence among subpopulations of migratory animals, and thus the applicability of metapopulation theory as a conceptual framework for understanding population dynamics, is much more difficult. Unlike nonmigratory species, subpopulations of migratory animals cannot be defined as synonymous with geographic areas. Groups of migratory birds that are geographically separate at one part of the annual cycle may occur together at others, but co-occurrence in time and space does not preclude the demographic independence of subpopulations. I suggest that metapopulation theory can be applied to migratory species but that understanding the degree of subpopulation independence may require information about both spatial distribution throughout the annual cycle and behavioral mechanisms that may lead to subpopulation demographic independence. The key for applying metapopulation theory to migratory animals lies in identifying demographically independent subpopulations, even as they move during the annual cycle and potentially co-occur with other subpopulations. Using examples of migratory bird species, I demonstrate that spatial and temporal modes of subpopulation independence can interact with behavioral mechanisms to create demographically independent subpopulations, including cases in which subpopulations are not spatially distinct in some parts of the annual cycle.*

Aplicación de la Teoría de Metapoblación en la Conservación de Aves Migratorias

Resumen: *La teoría de la metapoblación ha demostrado ser útil para el entendimiento de la estructura poblacional y de las dinámicas de muchas especies de interés para la conservación. Sin embargo, el concepto de metapoblación ha sido aplicado casi exclusivamente a especies no migratorias, para las cuales la independencia demográfica de la subpoblación (un requerimiento para una metapoblación definida de manera clásica) está explícitamente relacionada con la distribución geográfica y las probabilidades de dispersión. La definición del grado de independencia demográfica entre subpoblaciones de animales migratorios, y por lo tanto su aplicabilidad a la teoría de la metapoblación como un marco de trabajo conceptual para el entendimiento de dinámicas poblacionales, es mucho más difícil. A diferencia de las especies no migratorias, las subpoblaciones de animales migratorios no pueden ser definidas como sinónimas de áreas geográficas. Grupos de aves migratorias que están separadas geográficamente en una parte del ciclo de vida pueden estar juntos en otras. Sin embargo, la co-ocurrencia en tiempo y espacio no excluye la independencia demográfica de las subpoblaciones. Sugiero que la teoría metapoblacional puede ser aplicada a especies migratorias, pero que el entendimiento del grado de independencia subpoblacional puede requerir de información referente tanto a la distribución espacial a lo largo de un ciclo anual como a los mecanismos conductuales que pueden conducir a la independencia demográfica de la subpoblación. La clave para aplicar la teoría metapoblacional a especies migratorias de animales radica en la identificación de subpoblaciones demográficamente independientes, aún cuando estas se muevan durante el ciclo anual y potencialmente co-ocurran con otras subpoblaciones. Mediante el empleo de ejemplos de especies de aves migratorias, demuestro que los modos espa-*

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ciales y temporales de independencia subpoblacional pueden interactuar con los mecanismos conductuales para crear subpoblaciones demográficamente independientes, incluyendo casos donde las subpoblaciones no difieren espacialmente en algunas etapas de su ciclo anual.

Introduction

Understanding population structure is critical for the conservation of wildlife species, both with respect to defining units of conservation concern (e.g., evolutionarily significant units and management units; Moritz 1994) and identifying demographic constraints to population viability or recovery. Metapopulation theory offers one conceptual framework for considering population structure and demography. Metapopulation theory, as conceived by Levins (1970) and elaborated by others (e.g., Hanski & Gilpin 1991, 1996; McCullough 1996), addresses the demography of distinct subpopulations (specifically, extinction probabilities), interactions among subpopulations (dispersal and recolonization), and, ultimately, persistence of the aggregate of subpopulations, or the metapopulation. Metapopulation theory has been applied increasingly to conservation problems, in particular in cases where species' ranges have been fragmented by habitat alteration by humans (McCullough 1996).

In both concept and application, metapopulation theory has focused almost exclusively on nonmigratory species. Although often applied to mammals, metapopulation theory also has proven useful in studies of population dynamics of resident avian species (e.g., Temple 1992; Wootton & Bell 1992; Gutiérrez & Harrison 1996; J. N. Smith et al. 1996; Stith et al. 1996). When applied to migratory birds, metapopulation theory has been invoked in considerations of interactions among groups of birds from disjunct breeding areas (Buckley & Downer 1992; Opdam et al. 1994; Lindberg et al. 1998).

Missing from the literature, however, are considerations of the degree of demographic independence among subpopulations—and thus of the applicability of metapopulation theory—throughout the entire annual cycle of migratory birds. For metapopulation theory to apply, in its classical definition, (1) subpopulations must be sufficiently independent that extinction of a subpopulation can occur irrespective of the demographics of other subpopulations and (2) dispersal among subpopulations must be frequent enough that recolonization of extinct subpopulations can occur. For the purposes of this paper, I define *demographic independence* as instances in which subpopulations meet these criteria and *demographic panmixia* as cases in which subpopulations, in the metapopulation context, do not exist because of a lack of independence of extinction probabilities. Subpopulations are defined as groupings of birds that are demographically independent; the term applies

to either breeding or wintering areas. Instances of demographically distinct groups with no probability of exchange of individuals would be appropriately described as isolated and cannot be considered under the metapopulation construct. The term *metapopulation* often is inappropriately considered synonymous with fragmented populations. For understanding population dynamics and prescribing conservation actions, however, classically defined metapopulations differ considerably from populations with disjunct distributions. I explore application of the original metapopulation concept to understanding population dynamics of groups of migratory birds through (1) consideration of difficulties in identification and definition of subpopulations of migratory birds and (2) consideration of the mechanisms that could lead to subpopulation demographic independence throughout the annual cycle.

Contrasting Nonmigratory and Migratory Species

For nonmigratory species, the degree of demographic independence is explicitly related to geography, and exchange of individuals is simply a function of dispersal probabilities among geographic areas. In the typical metapopulation example (Fig. 1), subpopulations are spatially distinct and co-occurrence of individuals from different subpopulations occurs only with dispersal. The demographic processes affecting groups of animals within each area determine the extinction probabilities of subpopulations. If rates of dispersal are high enough to preclude extinction within each area, demographic panmixia exists, and the metapopulation concept does not apply.

Applying metapopulation theory to migratory animals becomes a much more difficult problem. For nonmigratory species, subpopulation and area are synonymous in a metapopulation context (Fig. 1); this is not the case for migratory animals. Subpopulations of migratory animals by definition are not spatially static. When applying metapopulation theory to migratory bird conservation, it is critical to keep in mind that areas per se are not the units of conservation concern or the units that form a metapopulation; rather, the units are subpopulations of animals. For migratory species, definition of these units cannot be inferred solely from geographic isolation and dispersal probabilities at a single life stage. Groups of animals that are spatially distinct at some parts of the annual cycle may occur together at others. Nevertheless,

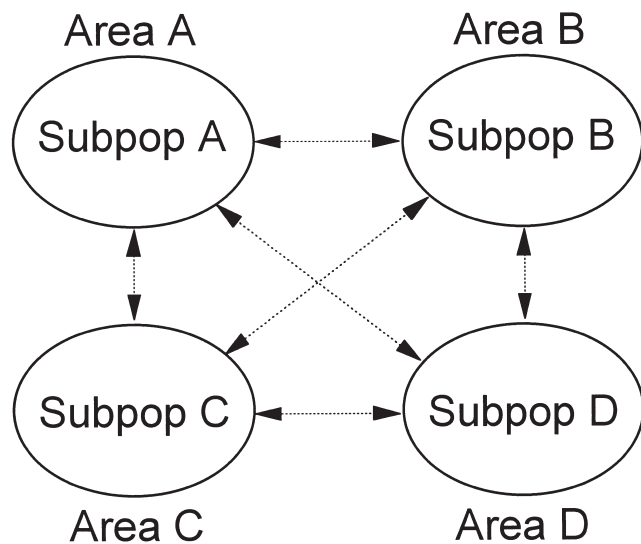


Figure 1. Metapopulation structure of nonmigratory animals. Geographic area is exactly concordant with the bounds of defined subpopulations (ovals), and the exchange of individuals occurs through dispersal (dashed arrows).

co-occurrence in time and space during part of the annual cycle does not necessarily imply demographic panmixia. Further, factors leading to either demographic independence or panmixia can occur at all parts of the annual cycle of migratory birds.

Thus, the key questions regarding the applicability of metapopulation theory to migratory birds are (1) What groupings of individuals constitute demographically independent subpopulations? and (2) What mechanisms lead to demographic independence or panmixia throughout the annual cycle? I suggest that applicability of metapopulation theory as a conceptual framework for understanding the population structure and dynamics of migratory birds requires consideration of spatial, temporal, and behavioral factors that affect demographic independence throughout the year, something that has not been discussed in the literature.

Spatial and Temporal Modes of Demographic Independence

Although geography is not the only determinant of demographic independence in migratory birds, geographic isolation must occur at some critical stage in the annual cycle for demographically independent subpopulations to exist. In general, four scenarios of spatial and temporal dynamics of migratory birds during breeding and winter are possible (Fig. 2). These are obviously simplifications of the annual cycle; they don't include staging, molting, or migration area, for example. But most of the

temporal and behavioral factors that could lead to subpopulation independence occur during breeding and wintering, and these generalizations can be extended to other periods.

The situation when winter panmixia and distinct breeding areas occur (Fig. 2a) could be considered a metapopulation if there is some behavioral mechanism that results in demographically independent breeding subpopulations—that is, if these subpopulations have independent extinction probabilities. This is clearly different from the typical nonmigratory metapopulation (Fig. 1) in that individuals co-occur during winter. Co-occurrence, however, does not preclude the demographic independence of breeding subpopulations, in which case metapopulation theory can apply.

The situation when distinct winter areas and breeding-area panmixia occur (Fig. 2b) is similar to the previous one and could function as a metapopulation if behavioral mechanisms exist that create demographically independent wintering subpopulations. In other words, even though all individuals share a breeding area, demographically independent subpopulations could exist on wintering areas if, for example, winter area philopatry is high. The applicability of metapopulation models is not limited to the breeding season. Subpopulation independence, whether on breeding or wintering areas, can have important implications for metapopulation dynamics and persistence.

For migratory birds, distinct winter and breeding areas (Fig. 2c) is the situation that most closely parallels the conventional, nonmigratory metapopulation model. Linked breeding and wintering areas could represent distinct subpopulations, with occasional exchange of individuals through dispersal at any part of the annual cycle. If breeding and wintering areas are not linked—if, for example, birds in a wintering area come from several breeding areas (or vice versa)—the metapopulation may function as in the previous two examples, or the population may be demographically panmictic and thus not qualify as a metapopulation at all.

The situation when winter and breeding-ground panmixia occurs (Fig. 2d) is analogous to a single, panmictic nonmigratory subpopulation. There is no mechanism for subpopulation demographic independence, so metapopulation theory cannot apply.

Behavioral Mechanisms of Demographic Independence of Subpopulations

While three of the examples of spatial and temporal dynamics described above have the potential to create demographic independence, none of them guarantees it. Spatial and temporal segregation must interact with behavioral mechanisms to result in independence. The

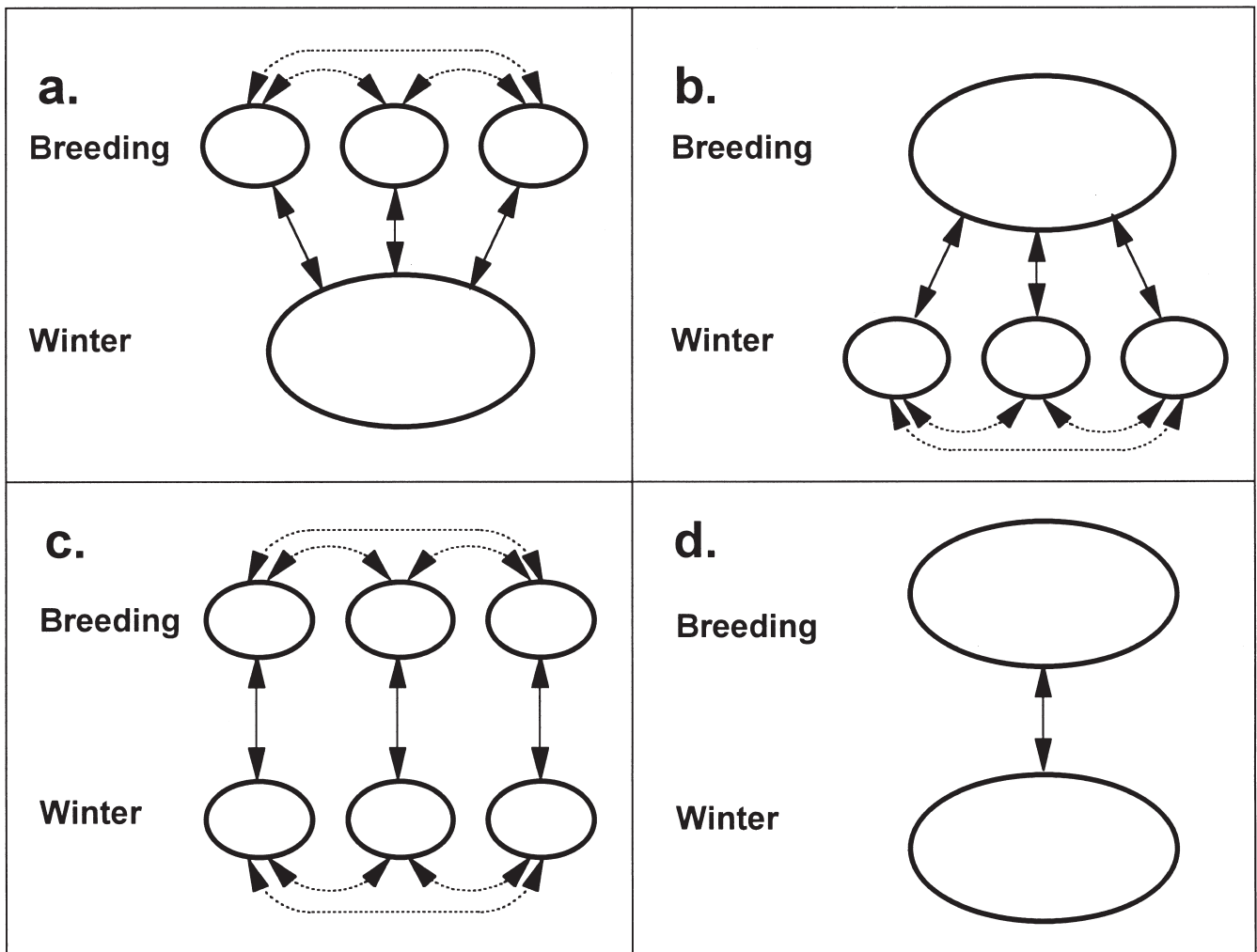


Figure 2. Four scenarios of spatial and temporal dynamics of migratory birds between breeding and wintering areas. Ovals represent geographically distinct groups, solid arrows represent migration, and dashed arrows represent dispersal.

primary behavioral mechanisms in this regard are philopatry and dispersal. Philopatry is the probability of returning annually to a specific geographic area during a particular life-cycle stage. Species with high levels of philopatry, either natal or annual, are more likely to have demographically independent subpopulations because of limited exchange of individuals among subpopulations. Dispersal can be considered the inverse of philopatry and, in this context, can refer to the probability of animals moving among subpopulations within a period of the annual cycle. It is important to remember that metapopulations must have limited exchange of individuals, such that subpopulations are demographically independent, but enough exchange that extinct subpopulations have some probability of being recolonized. Numerous other behavioral mechanisms—the timing of pair bonding, for example—can secondarily affect philopatry or dispersal and thus subpopulation indepen-

dence. Case-by-case assessment of philopatry, dispersal, mating systems, and other behavioral characteristics is necessary when the applicability of metapopulation models are under consideration.

Examples

I offer examples of migratory bird species that illustrate interactions between spatial, temporal, and behavioral mechanisms of subpopulation independence and their relevance to the application of metapopulation theory to conservation of migratory birds. These examples represent various geographic and numeric scales, from local subpopulations with dozens of individuals to continental populations with tens of thousands. The applicability of metapopulation theory does not depend on scale but rather on population structure. If the criteria for demo-

graphically independent subpopulations are met, metapopulation theory can apply. Migratory birds have the capacity to disperse over large geographic scales, and because the metapopulation concept depends on the scale of interactions among subpopulations (i.e., dispersal distances), metapopulations of migratory birds may exist among geographically extensive subpopulations.

Spectacled Eiders (*Somateria fischeri*) are sea ducks that breed in three main areas: arctic Russia, the Yukon Delta (western Alaska), and Alaska's North Slope (Bellrose 1980; Stehn et al. 1993). The entire population is thought to winter in the Bering Sea (Bellrose 1980; Petersen et al. 1995). Dramatic population declines in western Alaska (Stehn et al. 1993) prompted the listing of Spectacled Eiders as threatened in North America. For their conservation, it is important to know whether breeding areas represent subpopulations of a metapopulation (Fig. 2a) or if the entire population is demographically panmictic (Fig. 2d). As in other sea ducks, formation of pair bonds among Spectacled Eiders occurs during winter, and males likely follow females to their choice of nesting area (Rohwer & Anderson 1988). These behavioral traits might lead one to assume demographic panmixia, but female natal and annual philopatry is apparently high: mitochondrial DNA haplotype frequencies differ among breeding areas (K. Scribner, unpublished data). These genetic data suggest demographic independence of the females among subpopulations. Because subpopulations obviously cannot persist without females, breeding subpopulations can be considered distinct and demographically independent, despite the co-occurrence of birds during winter (Fig. 2a). With occasional female dispersal among breeding areas, this could be considered a metapopulation and managed as such.

A different situation is exemplified by Bristle-thighed Curlews (*Numenius tabitensis*). These curlews breed in two areas of Alaska, likely representing distinct populations (Marks & Redmond 1994). Each of these groups—which I assume to be completely distinct for the purposes of this example, based on high breeding-site fidelity (R. Gill, personal communication)—may be considered a metapopulation (Fig. 2b). From the breeding area, Bristle-thighed Curlews migrate to islands and atolls scattered throughout the South Pacific (Marks & Redmond 1996). Fidelity to specific wintering islands is high but not absolute, particularly for young birds (Marks & Redmond 1996), suggesting the potential for both demographic independence and recolonization. In fact, island extinctions and recolonizations have been recorded for this species (Marks & Redmond 1994), suggesting that a metapopulation model based on wintering subpopulations is both appropriate and useful for understanding population dynamics. The primary conservation concern for Bristle-thighed Curlews are threats to wintering birds from humans and introduced animals on some islands (Gill & Redmond 1992; Marks & Redmond

1994). Understanding population dynamics in the context of metapopulation theory will assist in assessment of population viability and threats to this species.

Similarly, Kirtland's Warblers (*Dendroica kirtlandii*) consist of a single breeding population with widely dispersed, distinct wintering subpopulations in the Bahama Archipelago (Sykes & Clench 1998). Although there are not sufficient data to describe winter fidelity and dispersal dynamics, it seems plausible that the Kirtland's Warbler population is structured as a metapopulation (Fig. 2b). Drought and introduced cats may affect subpopulations on some islands, but metapopulation dynamics may allow population persistence. The curlew and warbler situations offer clear examples of winter-based metapopulations, because islands represent discrete habitat patches; but the same process may occur for other species with high winter-site fidelity and panmictic breeding distributions.

The situations in which there are distinct winter and breeding areas (Fig. 2c) and winter and breeding-ground panmixia (Fig. 2d) are analogous to nonmigratory species with disparate and panmictic distributions, respectively. For example, Whooping Cranes (*Grus americana*) have two distinct subpopulations, one breeding at Wood Buffalo National Park in Canada and wintering along the Gulf of Mexico at Aransas National Wildlife Refuge and an "experimental" population breeding at Grays Lake National Wildlife Refuge, Idaho, and wintering at Bosque del Apache National Wildlife Refuge, New Mexico (McMillen 1988). This situation—distinct winter and breeding areas (Fig. 2c)—could be considered a metapopulation with dispersal (or translocation) between subpopulations. North American geese offer another example of this population structure because they tend to have relatively high levels of philopatry to both wintering and breeding areas (Anderson et al. 1992).

Northern Pintails (*Anas acuta*) nest across North American prairies, parklands, and tundra (Bellrose 1980) and winter throughout the southern half of the continent (Hestbeck 1993) and into Central and South America. Pintails are relatively abundant but are one of the few waterfowl species that are below target goals set by the North American Waterfowl Management Plan (Canadian Wildlife Service & U.S. Fish and Wildlife Service 1986). Pintails are thought to be highly nomadic, moving extensively among nesting areas (Johnson & Grier 1988). Poor conditions in the prairies result in large-scale movements to northern areas (Hansen & McKnight 1964; R. I. Smith 1970; Henny 1973; Derksen & Eldridge 1980). Although movements do not necessarily result in incorporation into functional subpopulations (Slatkin 1987; Avise et al. 1992), mtDNA analyses demonstrate that pintails breeding in North America are genetically panmictic (Cronin et al. 1996), suggestive of demographic panmixia in conjunction with direct evidence of low breeding-area fidelity. Furthermore, wintering areas

include birds from breeding areas all over the continent, and winter-site fidelity is generally low (Fedynich et al. 1989; Hestbeck 1993). Northern Pintails provide an example of panmixia at all scales of consideration (Fig. 2d), and thus metapopulation theory should not be applied to this case.

Conclusions and Conservation Implications

Metapopulation theory can be a powerful tool for the conservation of birds (Opdam 1991; Opdam et al. 1994), including migratory birds, providing a conceptual framework within which dynamics of some populations can be considered or predicted. Determining whether a metapopulation structure exists for migratory species is confounded by difficulties in identifying demographically independent subpopulations. Fragmented or disjunct groups of animals do not necessarily constitute a metapopulation. Similarly, co-occurring migratory animals cannot be assumed to be part of the same demographically panmictic group. Identification of groups of animals as demographically independent subpopulations within a metapopulation, as totally disjunct populations, or as a part of a demographically panmictic population has important ramifications for defining conservation strategies. As my examples demonstrate, the conceptual framework of metapopulation theory can apply to some species of migratory birds. To know whether metapopulation theory applies, more information may be needed for migratory species than for nonmigratory species. Geographic isolation or mixing and measures of dispersal distance at a single life stage may not be enough. Other parameters that need to be determined to understand the degree of subpopulation demographic independence may include distribution throughout the annual cycle (spatial and temporal segregation), the behavioral mechanisms of segregation, and, particularly, the interaction between spatial, temporal, and behavioral mechanisms.

In some cases, metapopulation structure can be defined during only part of the annual cycle, as in distinct breeding areas that meet the criteria for demographically independent subpopulations (Buckley and Downer 1992; Opdam et al. 1994). In these cases, the metapopulation concept can aid in population conservation. Population structure during one part of the annual cycle, however, cannot indicate population structure and interactions during other parts of the year. In particular, a population that is demographically panmictic during one part of the year may be structured as a metapopulation during another period. Furthermore, population structure during the breeding season should not be considered the definitive structure for the population. The population structure during winter may be as important,

or more so, than that during breeding. The examples of Bristle-thighed Curlews and Kirtland's Warblers demonstrate how the application of metapopulation theory during nonbreeding seasons can have important conservation implications for species of concern. It runs contrary to a traditional temperate, Northern Hemisphere viewpoint to consider population structure to be defined during nonbreeding periods, but there is no reason that breeding areas should take precedence. Nothing in the definition of the metapopulation concept refers to breeding area, and I argue that the application of metapopulation theory to migratory birds should focus on defining demographically independent subpopulations, which may exist during any part of the annual cycle.

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